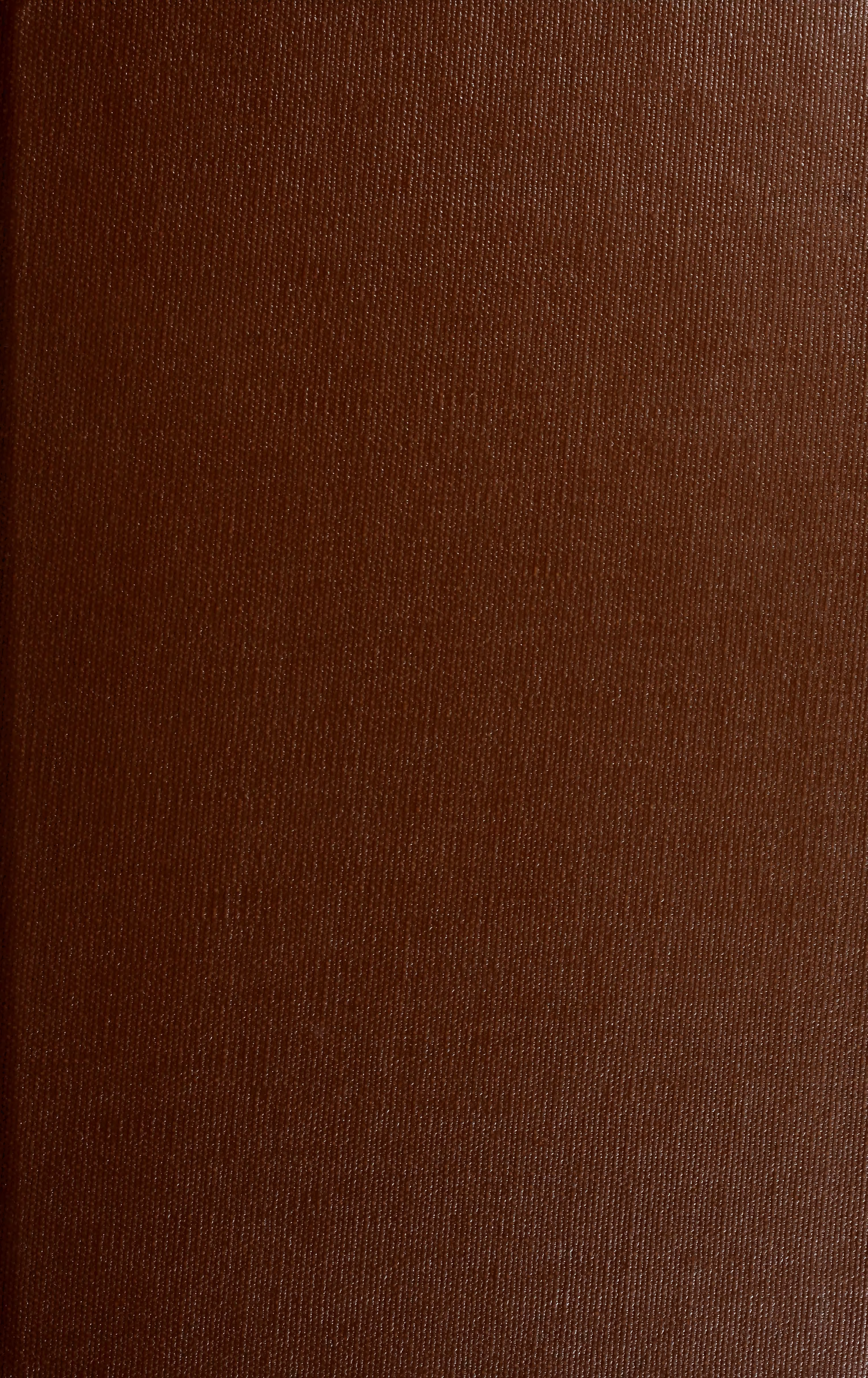
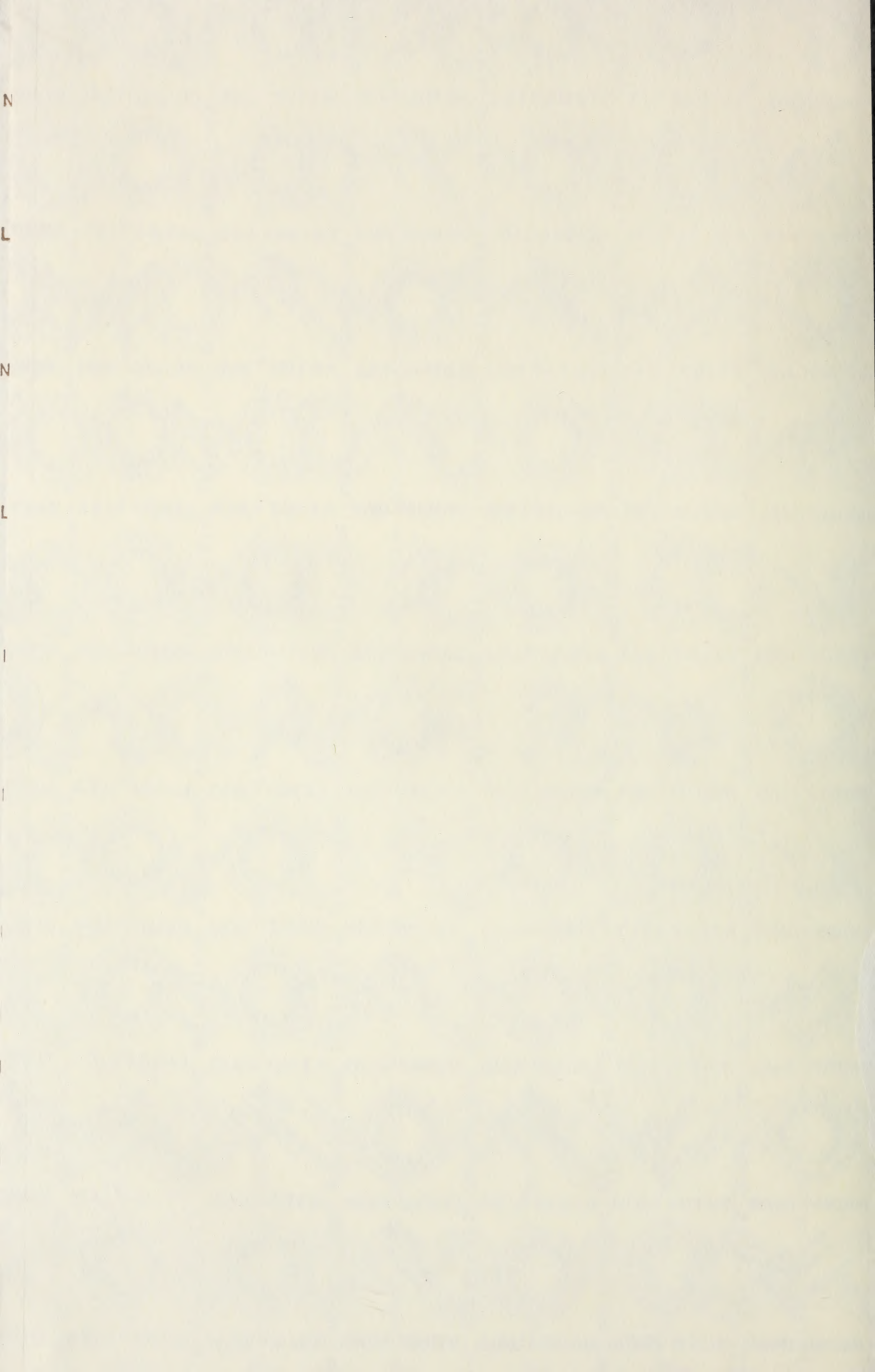





SMITHSONIAN INSTITUTION LIBRARIES
SMITHSONIAN INSTITUTION WASHINGTON DC



ZEITSCHRIFT FÜR SÄUGETIERKUNDE

INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde

Volume 54, 1989 ISSN 0044–3468

Mit 159 Abbildungen



Verlag Paul Parey Hamburg und Berlin

Wissenschaftliche Originalarbeiten

Wissenschaftliche Kurzmitteilungen

Bekanntmachungen

Buchbesprechungen

This journal is covered by Biosciences Information Service of Biological Abstracts, and by Current Contents (Series Agriculture, Biology, and Environmental Sciences) of Institute for Scientific Information

ISSN 0044-3468 54 (1–6) 1–408 (1989)

Vol. 54 (1), 1–64, Februar 1989 ISSN 0044-3468 C 21274 F

ZEITSCHRIFT FÜR SÄUGETIERKUNDE

INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde





Verlag Paul Parey Hamburg und Berlin

This journal is covered by Biosciences Information Service of Biological Abstracts, and by Current Contents (Series Agriculture, Biology, and Environmental Sciences) of Institute for Scientific Information

---

Die Zeitschrift für Säugetierkunde veröffentlicht Originalarbeiten und wissenschaftliche Kurzmitteilungen aus dem Gesamtgebiet der Säugetierkunde, Besprechungen der wichtigsten internationalen Literatur sowie die Bekanntmachungen der Deutschen Gesellschaft für Säugetierkunde. Verantwortlicher Schriftleiter im Sinne des Hamburgischen Pressegesetzes ist Prof. Dr. Harald Schliemann.

Zusätzlich erscheint einmal im Jahr ein Heft mit den Abstracts der Vorträge, die auf der jeweiligen Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde gehalten werden. Sie werden als Supplement dem betreffenden Jahrgang der Zeitschrift zugeordnet. Verantwortlich für ihren Inhalt sind ausschließlich die Autoren der Abstracts.

Manuskripte: Manuskriptsendungen sind zu richten an die Schriftleitung, z. Hd. Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Biologie-Zentrum, Neue Universität, Olshausenstr. 40–60, D-2300 Kiel. Für die Publikation vorgesehene Manuskripte sollen gemäß den „Redaktionellen Richtlinien“ abgefaßt werden. In ihnen finden sich weitere Hinweise zur Annahme von Manuskripten, Bedingungen für die Veröffentlichung und die Drucklegung, ferner Richtlinien für die Abfassung eines Abstracts und eine Korrekturzeichentabelle. Die Richtlinien sind auf Anfrage bei der Schriftleitung und dem Verlag erhältlich.

Sonderdrucke: Anstelle einer Unkostenvergütung erhalten die Verfasser von Originalbeiträgen und Wissenschaftlichen Kurzmitteilungen 50 unberechnete Sonderdrucke. Mehrbedarf steht gegen Berechnung zur Verfügung, jedoch muß die Bestellung spätestens mit der Rücksendung der Korrekturfahnen erfolgen.

Mit zwei Beilagen des Verlages Paul Parey

Fortsetzung 3. Umschlagseite

 Verlag: Paul Parey, Hamburg und Berlin. Anschriften: Spitalerstr. 12, D-2000 Hamburg 1; Lindenstr. 44–47, D-1000 Berlin 61. – Printed in Germany by Westholsteinische Verlagsdruckerei Boyens & Co., D-2240 Heide/Holst.

Z. Säugetierkunde 54 (1989) 1–8

ISSN 0044-3468

Echolocation calls of Malaysian bats

By K.-G. Heller

Institut für Zoologie, Universität Erlangen-Nürnberg

Receipt of Ms. 3. 8. 1987

Abstract

The echolocation calls of free-flying bats of the genera *Tylonycteris, Glischropus, Hesperoptenus, Myotis, Emballonura* and *Taphozous* were recorded in the field and examined in their pattern of frequency change over time (fig. 1, 3). Except *Myotis hasseltii* (pure frequency modulated calls) the calls of all vespertilionids consist of a frequency modulated beginning and a nearly constant frequency end (fm-cf-calls). *Hesperoptenus blanfordi* emits alternately signals with different cf-parts (32 and 40 kHz). The function of this behaviour is discussed especially with regard to the range of the echolocation system. The species of the genus *Taphozous* show like all other members of this genus studied so far nearly constant frequency calls. Additionally to the strongest first harmonic here the fundamental and higher harmonics can be observed. The calls of *Emballonura monticola* are also only weakly frequency modulated.

Introduction

The echolocation of bats represents one of the very few active orientation systems used by animals. Additionally to the commonly observed adaptations of sensory organs to environmental conditions here adaptions on the transmitter side are to be expected, too. Examples from morphology are the complicated nose-leaves of many Rhinolophidae and Phyllostomidae. They are most probably used for beaming the sound in certain directions. Many details of their structure, however, remain unexplained.

Adaptations to ecological conditions are also found in the echolocation signals themselves. Depending on foraging sites and strategies (e.g. close to vegetation, in open space) calls of completely different structure are used (Neuweiler 1983; Habersetzer 1986). To understand the regularities involved the sonar signals of many species living and hunting in different habitats have to be examined together with detailed studies of flight and echolocation behaviour of single species.

Up to now only the echolocation calls of bats living in temperate zones have been studied relatively thoroughly (Europe: Ahlen 1981; Weid and v. Helversen 1987; North America: Fenton and Bell 1981; and many other studies). From tropical areas, rich in bat species, however, few observations are available. Detailed, comparative studies of free-flying animals have been carried out only in India (Neuweiler 1983; Habersetzer 1986), Zimbabwe (Fenton and Bell 1981) and Australia (Fenton 1982).

In the following the echolocation calls of 8 species (6 genera) of the families Vespertilionidae and Emballonuridae are described. Except one they occur syntopic in Ulu Gombak, Malaysia. Two genera *(Glischropus, Hesperoptenus)* have never before been studied bioacoustically, species of further two *(Tylonycteris, Emballonura)* have been recorded only hand-held or flying in the laboratory (Novick 1958; Grinnell and Hagiwara 1972), where the call structure is very different from signals used during foraging.

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5401-0001 $ 02.50/0

Methods

Most bats (exceptions see below) were observed and captured (with mist nets) between Feb 28th and Mar 24th 1984 at the Ulu Gombak Field Study Centre (3°20′ N, 101°46′ E) of the University of Malaya near Kuala Lumpur. *Myotis hasseltii* was captured at Kuala Selangor, *Taphozous melanopogon* was observed at the Batu Caves (further details see Heller and Volleth 1988).

The echolocation and social calls were recorded with a self-built condensor microphone (similar to e.g. QMC SM1) and amplifier on a modified video recorder. With this combination frequencies up to 200 kHz could be registered. The frequency response during recording, however, was not exactly known and certainly not flat over the whole range.

Due to this microphone characteristic, the frequency-dependent atmospheric attenuation of sound (the higher the frequency, the stronger the attenuation) and different distances of the flying animals, no definite statements can be made about sound pressure levels. This holds true also for the relations of sound pressure level between fundamental and harmonics resp. between harmonics, and for the highest detectable frequency at the beginning of the call in steeply frequency modulated calls. It will be lower with increasing distance, even if the call emitted by the bat does not change.

If possible the frequency of constant frequency parts is used for characterizing a species. In the Vespertilionini with cf-call endings one has to consider that in short calls the frequency of short calls is higher than that expected from shortening longer calls (Weid and v. Helversen in prep). Additionally inaccuracies result from the Doppler effect caused by the flight velocity of the bat. In *Saccopteryx bilineata* (cf-frequency 47 kHz) it comes to 2–3 kHz (Pye 1978) for example.

For evaluation, certain sequences were recorded with a RACAL store DS tape recorder and after appropriate slow down (mostly 32×) analysed with a MOSIP-FFT-processor (Fa. MEDAV, D-8520 Erlangen-Buckenhof, Am Tennenbach 9). Some original prints are shown in fig. 5 (echoes and background noise eliminated with opaque white), for fig. 1 and 3 the signals were copied by hand.

Results and discussion

Family Vespertilionidae

Nearly all analysed calls come from captured and identified animals after releasing.

Members of the tribe Vespertilionini

The four species of this group *Tylonycteris pachypus, T. robustula, Glischropus tylopus, Hesperoptenus blanfordi* were frequently caught simultaneously (see fig. 1 in Heller and Volleth 1988) in the same mist net. *Glischropus tylopus*, however, was rarer than the other three species. More detailed observations of the hunting behaviour are not available. All species show the tribe typical fm-cf-call structure (Weid and v. Helversen 1987): a steeply modulated beginning (fm-part) is followed by a part in which the frequency decreases only very slowly (cf-part). The portion of each component varies widely according to the situation: during prey capture and close to obstacles the cf-part is reduced (up to complete disappearance), in open environments however almost pure cf signals can be used.

Additionally to the fundamental frequency, harmonics (mainly the first and the second) can be discerned. Nothing can be said, however, about their amplitude in relation to each other and their meaning (see Methods).

Tylonycteris pachypus (Temminck, 1840)

In the calls (duration 2–7,5 ms) of three animals examined the highest frequency at the beginning was found to be 125 kHz. It sweeps down to 58 kHz in short calls without distinct cf-part and to 50 kHz in long calls (fig. 1A). During a prey capture situation, which was assigned to this species on account of the preceding calls, no frequency shift at the end of the final buzz as in *Glischropus tylopus* (fig. 1H) could be observed (fig. 1F).

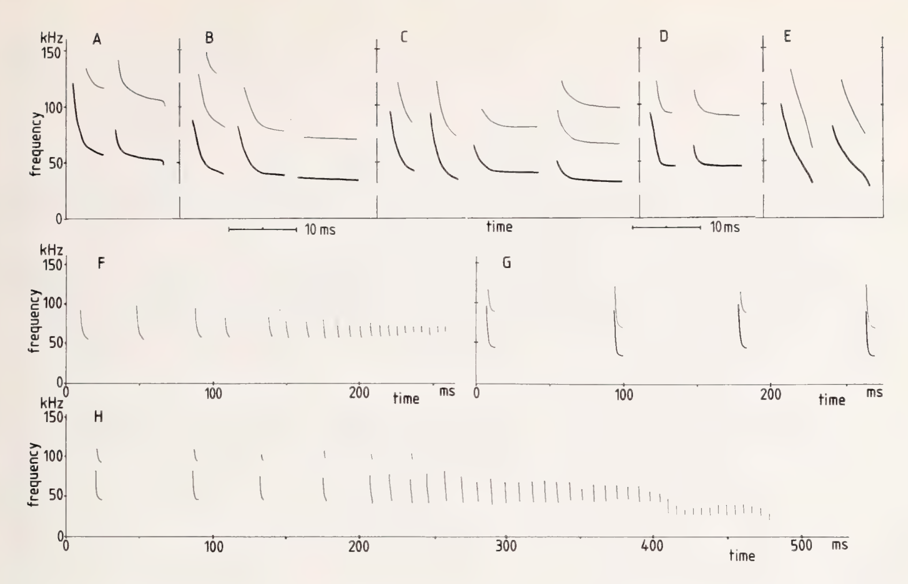


Fig. 1. Single echolocation calls of A: *Tylonycteris pachypus;* B: *Tylonycteris robustula;* C: *Hesperoptenus blanfordi;* D: *Glischropus tylopus;* E: *Myotis hasseltii;* F: feeding buzz of *Tylonycteris pachypus;* G: sequence of alternating high and low calls of *Hesperoptenus blanfordi;* H: feeding buzz of *Glischropus tylopus*

Tylonycteris robustula Thomas, 1915

The calls (duration 2–8,5 ms) are similar in their structure to *T. pachypus*, but lower in frequency. They start frequently at about 90–100 kHz and sweep down to 48 kHz in short and 40 kHz in long signals (fig. 1B). In very long calls the frequency may reach 35 kHz. The pattern of the frequency modulation is relatively variable (16 animals studied).

The intervals between the calls show a sharp peak between 70 and 80 ms and a broad side peak at about twice that time (fig. 2). In some sequences one can easily observe that sometimes calls are omitted so that the call interval doubles.

Glischropus tylopus (Dobson, 1875)

In contrast to the *Tylonycteris* species here the frequency sweeps at the beginning are very steep and do not vary much (3 animals examined). The length of the following cf-part (call duration 3–7 ms) is variable, its final frequency, however, relatively constant. The call starts at about 95 kHz, the frequency of the cf-part lies between 45 and 49 kHz (fig. 1D). Only in final buzzes calls of deviating structure can be observed. Fig. 1H shows an unusually long feeding buzz. In its last calls a frequency shift downwards can be observed as it is known from several other Vespertilionidae (e.g. *Pipistrellus kuhlii* Schnitzler 1984). Another final buzz of the same animal is considerably shorter and lacks such a frequency change.

Hesperoptenus blanfordi (Dobson, 1877)

Unusual for Vespertilionidae, this species shows two call types with similar frequency modulation but different frequencies, which frequently change in a regular way (fig. 1G). This alternation could be heard in 9 of 11 animals after releasing, in the remaining two only high frequency calls could be observed.

The high frequency pulses (duration 3–9 ms) started at about 105 kHz at the maximum and ended between 40 and 45 kHz, the low frequency calls (duration 3–10 ms) started also

at 105 kHz, but swept down to 31–37 kHz (rarely in short calls only to 40 kHz). The difference in frequency between two successive calls was 8+ 1,5 kHz (x+ SD; range 5–11 kHz; n = 28 pairs). Alternation occurred in short and long calls (s. fig. 1C), mostly, however, in a given pair the higher call was a little bit shorter than the lower one.

An alternating change between two call types is until now known only in some Emballonuridae (Pye 1973) and *Barbastella barbastellus* (Ahlen 1981). In *Nyctalus noctula* frequently call pairs can be observed with the first call being higher in frequency than the second (Miller and Degn 1981; Ahlen 1981).

In emballonurids Pye (e.g. 1973) assumes that alternating is used as a certain Doppler effect compensation. The frequency difference of 2–3 kHz found there does not disprove this hypothesis saying that the echo of the low frequency call is received at the frequency of the higher call. A difference of 8 kHz, however, would require extremely high flight speeds never reached by *Hesperoptenus blanfordi.*

In view of the great frequency difference observed here one can assume that the two calls are used for different distances. Because of the frequency-dependent attenuation the range of the low calls is considerably longer than that of the high. At 25 °C and 25 % rel. humidity the atmospheric attenuation amounts to 1.2 dB/m for 40 kHz, but only to 0.7 dB/m for 32 kHz (Lawrence and Simmons 1982). The low frequency calls accordingly range at the maximum about 30 m compared with 20 m of the high calls (110 dB SPL call amplitude, an ideal, large reflector and a hearing threshold of 0 dB SPL; according to Lawrence and Simmons 1982).

This hypothesis is supported by the distribution of the call intervals (fig. 2). In contrast to similar sized *Tylonycteris robustula* here the side peak at longer intervals is much more prominent. A slight error, however, may result from the fact that from distant animals only low calls could be recorded. But if the intervals between low and high calls are examined separately, one finds that additionally to the alternating use high calls are emitted in short intervals (e.g. during take-off), which correspond well to the call intervals in *Tylonycteris robustula* (fig. 2) and in other small Vespertilionini (Ahlen 1981). Between

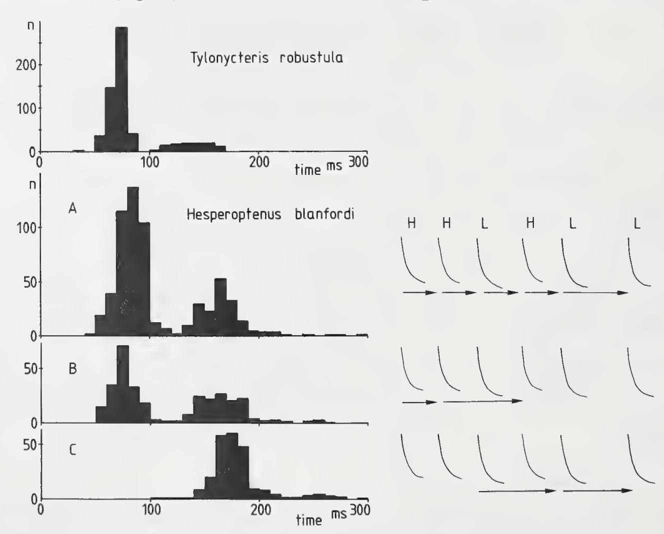


Fig. 2. Call intervals in *Tylonycteris robustula* (625 intervals, 20 sequences, 16 animals) and *Hesperoptenus blanfordi* (618 intervals, 13 sequences, 11 animals). A: intervals irrespectivly of call structure; B: intervals exclusively between high frequency calls; C: intervals exclusively between low frequency calls. At the right the different intervals are indicated schematically by arrows (H: high frequency call, L: low frequency call)

two low calls, however, there is always a long interval (fig. 2C). In some cases it was evident that the expected high call between two low pulses was missing.

The frequency of the low calls of *Hesperoptenus blanfordi* is unusually low for its body size. The species lies in weight and condylobasal length between *Tylonycteris pachypus* and *Glischropus tylopus* on the one hand and *Tylonycteris robustula* on the other hand. Assuming a similar correlation between body size and call frequency as in the European Vespertilioni (Weid and v. Helversen in prep.) and using the above mentioned species, a call frequency of about 40 kHz has to be expected. The same value is obtained, when the frequency is calculated by using condylobasal lengths and call frequencies of the European Vespertilionini (Weid and v. Helversen 1987). The extraordinary low calls with their long range have also late returning echoes (maximum: 180 ms for 30 m).

For interpretation of these results one has to consider the echolocation system of vespertilionid bats. The animals are confronted with some difficulties in echo recognition. First, they must avoid that the echo returns during the emission of the call. Therefore they shorten their calls when approaching prey or obstacles (e.g. Neuweiler 1984). In the same situation, however, they increase the call rate for exact localisation. A similar problem arises, when the echo returns very late thus interfering with the next call. Perhaps frequencies other than those emitted can be perceived during calling as is the case in Rhinolophidae (Neuweiler 1970). If the echo returns even later, the bat has to assign the echoes to the respective calls. In the last mentioned cases successive calls with different frequencies will be helpful.

Through alternating, *Hesperoptenus blanfordi* could thus combine the advantages of long ranging calls with the better target recognition of high frequency calls and of a fast pulse repetition rate (combining thus the strategies of *Lasionycteris noctivagans* and *Lasiurus cinereus* [Barclay 1986]). It only has to make sure that echoes of low frequency calls do not interfere with calls of the same type. The different cf-parts carrying most sound energy allow a reliable assignment of echoes and respective calls.

A hypothesis to the foraging behaviour could imply that *H. blanfordi* can detect large prey for which it is possibly spezialized (Heller and Volleth 1988) over great distances. With the high frequency calls it keeps in "ear" its closer surroundings. There are no indications to substantiate the considerations of Griffin (1971) who says that the call frequency is related to the acoustical contact to earth or to the height above ground. Accordingly *Hesperoptenus blanfordi* should fly especially high. The aspect ration index, a wing dimension that is correlated with flight velocity and altitude (Habersetzer 1986) is lower than in *Tylonycteris robustula* (Heller in prep.). Also, the low frequency calls are emitted in low altitude as well.

Myotis hasseltii (Temminck, 1840)

The species which forages closely to the water surface shows steeply frequency-modulated calls without any cf component. The calls (duration 2,5–5,5 ms) start at about 82–104 kHz and sweep down to 23–30 kHz (fig. 1E). They correspond thus very well with those of the closely related and ecologically very similar *Myotis adversus* (Thompson and Fenton 1982). Additionally to the fundamental the first harmonic can frequently be observed.

The envelope of a call often shows several minima as is observed in other species hunting closely to the water surface (e.g. Ahlen 1981). They most probably result from interferences at the microphone between the echo from the water surface and the call. In otherwise similar calls of an animal flying above ground (after releasing) where the echos are considerably weaker those minima could not be found.

Family Emballonuridae

Emballonura monticola (Temminck, 1838)

The attribution of the calls described here to *Emballonura monticola* is not verified by observations of identified animals. The peculiar call structure, however, excludes all other Malaysian species with great certainty. The characteristic frequency pattern – a slight increase is followed by a part decreasing very slowly at first and more steeply later on – indicates an emballonurid bat. In no other family such calls are known. From the four Malaysian species the three *Taphozous* can be ruled out because of their totally different calls (see below). *Emballonura monticola*, which is commonly found in Ulu Gombak, is thus the only remaining species.

Duration (6–8 ms) and frequency pattern of all recorded calls are very uniform except for the final buzzes. The highest frequency which can here be exactly determined lies between 48 and 51 kHz (fig. 3A). In contrast to the Vespertilionidae, the first harmonic is most accentuated, the fundamental can sometimes weakly be seen. More often the third and the weaker second harmonic are observed (in not overmodulated records). In the final buzz (fig. 3D) the narrow frequency range is only slightly enlarged. Sometimes here the fundamental is more pronounced.

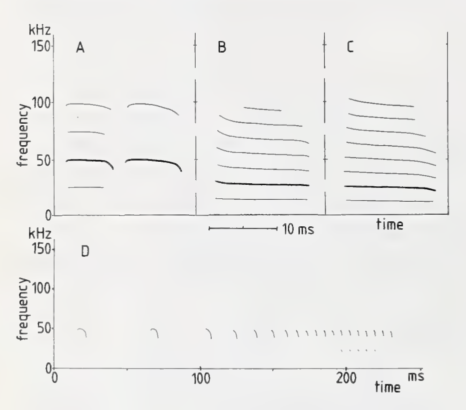


Fig. 3. Single echolocation calls of A: *Emballonura monticola;* B: *Taphozous melanopogon;* C: *Taphozous saccolaimus;* D: feeding buzz of *Emballonura monticola*

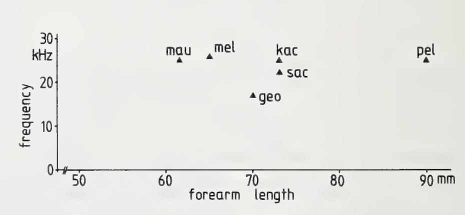


Fig. 4. Call frequency and forearm length in several *Taphozous* species (geo = *georgianus:* FENTON 1982; kac = *kachensis:* NEUWEILER 1983, HABERSETZER 1986; mau = *mauritianus:* FENTON et al. 1980; mel = *melanopogon:* NEUWEILER 1983, HABERSETZER 1986, this study; pel = *peli:* PYE 1980; sac = *saccolaimus;* forearm lengths according to KINGDON 1974, HABERSETZER 1986, HELLER and VOLLETH 1988, STRAHAN 1983

Genus *Taphozous*

The calls of the two *Taphozous* species *T. melanopogon* and *T. saccolaimus* are very similar in structure. Free flying, they both emit nearly constant frequency signals, which contain many harmonics known from other species of the genus (PYE 1980; FENTON 1982; NEUWEILER 1983; HABERSETZER 1986; only FENTON [1982] did not observe any harmonics). As in *Emballonura monticola* the first harmonic is the strongest component, the fundamental can often be weakly discerned, the upper harmonics decrease in amplitude corresponding to their number.

Comparing the call frequencies of the six *Taphozous* species studied so far one is surprised to see that there is no correlation to body size (fig. 4; forearm length used as measurement of body size; $y = 22.33 + 0.01x$; $r = 0.04$). This is in striking contrast to rhinolophid bats (genera *Rhinolophus* and *Hipposideros*; HELLER and v. HELVERSEN in prep.), several genera of vespertilionids (WEID and v. HELVERSEN in prep.) and other

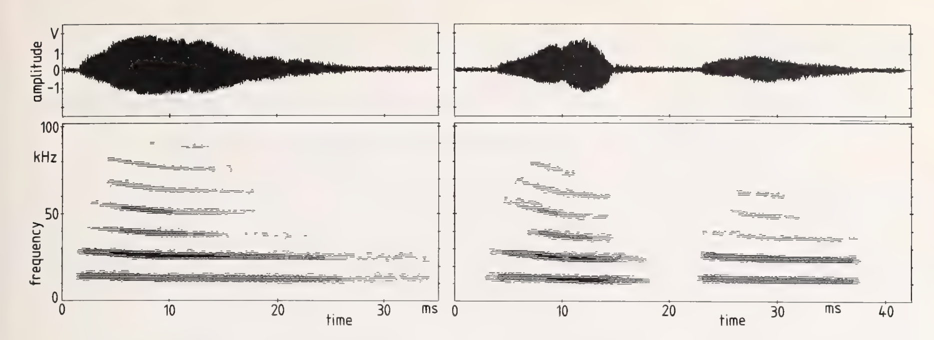


Fig. 5. Social calls of *Taphozous saccolaimus.* Notice the prominent fundamental

genera mentioned by Novick (1977). All these groups show a negative correlation between call frequency and body size (or forearm length). In the fast and high flying *Taphozous* body size apparently has less influence on echolocation than in the above mentioned genera.

Taphozous melanopogon Temminck, 1841

The species was recorded leaving the Batu Caves in the evening. The calls (duration 6–14 ms, rarely up to 17 ms) start at 26–30 kHz (first harmonic) and end with 24–26 kHz (average frequency drop 2 kHz; fig. 3B). In short calls occasionally a larger frequency range (31,5–23 kHz) is found and accordingly a steeper decrease. The call frequencies correspond well with the data of Neuweiler (1983) and Habersetzer (1986), the steep start and end components, however, mentioned by these authors are observed only very rarely.

Taphozous saccolaimus Temminck, 1838

The species was recorded leaving a hollow palm in the evening. The calls (duration mostly 8–14 ms, rarely 6–17 ms) start at 23–26 kHz (first harmonic) and sweep down to 20–24(–25) kHz (average frequency drop 2 kHz; fig. 3C).

Before taking off one animal emitted a series of social calls (fig. 5). They were similar to the echolocation calls but had a considerably more pronounced fundamental. The calls were composed of one or two elements, which were either clearly separated or fused (with a slight frequency increase in the central part).

Acknowledgements

I would like to thank Marianne Volleth, A. Liegl and J. Sachteleben for assistance in the field, Prof. Dr. O. v. Helversen, W. Metzner and R. Weid for critical review of the manuscript and Margot Ensenberger for help with the translation.

Zusammenfassung

Ortungsrufe malayischer Fledermäuse

Die Ortungsrufe freifliegender Fledermäuse aus den Gattungen *Tylonycteris, Glischropus, Hesperoptenus, Myotis, Emballonura* und *Taphozous* wurden im Feld aufgenommen und hinsichtlich Frequenzzusammensetzung und -verlauf untersucht (Abb. 1, 3). Abgesehen von *Myotis hasseltii* (vollständig frequenzmodulierte Laute) bestehen die Rufe der Vespertilioniden aus einem frequenzmodulierten Anfangsteil und einem fast konstantfrequentem Ende (fm-cf-Rufe). *Hesperoptenus blanfordi* stößt dabei alternierend Rufe mit verschieden hohen cf-Teilen aus (32 und 40 kHz). Die Funktion dieses Verhaltens wird besonders im Hinblick auf die Reichweite des Echoortungssystems diskutiert. Die Arten der Gattung *Taphozous* zeigen wie alle bisher untersuchten Vertreter dieser Gattung fast

konstantfrequente Rufe, in denen neben der amplitudenstärksten 1. Harmonischen oft auch die Grundschwingung sowie höherzahlige Oberwellen deutlich zu erkennen sind. Die Rufe von *Emballonura monticula* sind ebenfalls nur schwach frequenzmoduliert.

Literature

Ahlen, I. (1981): Identification of Scandinavian bats by their sounds. Rapp. 6 Swed. Univ. Agric. Sci. Dept. Wildl. Ecol., Uppsala.

Barclay, R. M. R. (1986): The echolocation calls of hoary *(Lasiurus cinereus)* and silver-haired *(Lasionycteris noctivagans)* bats as adaptations for long- versus short-range foraging strategies and consequences for prey selection. Can. J. Zool. **64**, 2700–2705.

Fenton, M. B. (1982): Echolocation calls and patterns of hunting and habitat use of bats (Microchiroptera) from Chillagoe, North Queensland. Aust. J. Zool. **30**, 417–425.

Fenton, M. B.; Bell, G. P. (1981): Recognition of species of insectivorous bats by their echolocation calls. J. Mammalogy **62**, 233–243.

Fenton, M. B.; Bell, G. P.; Thomas, D. W. (1980): Echolocation and feeding behavior of *Taphozous mauritianus* (Chiroptera: Emballonuridae). Can. J. Zool. **58**, 1774–1777.

Griffin, D. R. (1971): The importance of atmospheric attenuation for the echolocation of bats (Chiroptera). Anim. behav. **19**, 55–61.

Grinnell, A. D.; Hagiwara, S. (1972): Adaptations of the auditory nervous system for echolocation: studies of New Guinea bats. Z. vergl. Physiol. **76**, 41–81.

Habersetzer, J. (1986): Vergleichende flügelmorphologische Untersuchungen an einer Fledermausgesellschaft in Madurai. In: Biona-Report 5. Ed. by W. Nachtigall. Akad. Wiss. Mainz. Stuttgart, New York: G. Fischer, 75–104.

Heller, K.-G.; Volleth, M. (1988): Fledermäuse aus Malaysia. 1. Beobachtungen zur Biologie, Morphologie und Taxonomie. Senckenberg. biol. (in press).

Kingdon, J. (1974): East African mammals. Vol. II, A: Insectivores and bats. London, New York: Academic Press.

Lawrence, B. D.; Simmons, J. A. (1982): Measurements of atmospheric attenuation at ultrasonic frequencies and the significance for echolocation by bats. J. Acoust. Soc. Am. **71**, 585–590.

Miller, L. A.; Degn, H. J. (1981): The acoustic behaviour of four species of vespertilionid bats studied in the field. J. comp. Physiol. **125**, 67–74.

Neuweiler, G. (1983): Echolocation and adaptivity to ecological constraints. In: Neuroethology and behavioural physiology. Ed. by F. Huber and H. Markl. Berlin, Heidelberg, New York, Tokyo: Springer. pp. 280–302.

— (1970): Neurophysiologische Untersuchungen zum Echoortungssystem der Großen Hufeisennase *Rhinolophus ferrumequinum*. Z. vergl. Physiol. **67**, 273–306.

— (1984): Foraging, echolocation and audition in bats. Naturwissenschaften **71**, 446–455.

Novick, A. (1958): Orientation in palaeotropical bats. I. Microchiroptera. J. exp. biol. **138**, 81–153.

— (1977): Acoustic orientation. In: Biology of bats. Vol. III. Ed. by W. A. Wimsatt. New York, San Francisco, London: Academic Press. pp. 74–287.

Pye, J. D. (1973): Echolocation by constant frequency in bats. Period. biol. **75**, 21–26.

— (1978): Some preliminary observations on flexible echolocation systems. In: Proc. Fourth Int. Bat Res. Conf. Ed. by R. F. Olembo, J. B. Castelino and F. A. Mutere. Nairobi: Kenya Lit. Bureau. pp. 127–136.

— (1980): Adaptiveness of echolocation signals in bats. Trends in Neurosciences **3**, 232–235.

Thompson, D.; Fenton, M. B. (1982): Echolocation and feeding behaviour of *Myotis adversus* (Chiroptera, Vespertilionidae). Aust. J. Zool. **30**, 543–546.

Schnitzler, H.-U. (1984): The performance of bat sonar systems. In: Localization and orientation in biology and engineering. Ed. by Varju and H.-U. Schnitzler. Berlin, Heidelberg: Springer. pp. 211–224.

Strahan, R. (ed.) (1983): Complete book of Australian mammals. London, Sydney, Melbourne: Angus and Robertson.

Weid, R.; Helversen, O. v. (1987): Ortungsrufe europäischer Fledermäuse beim Jagdflug im Freiland. Myotis **25**, 5–27.

Author's address: Dr. Klaus-Gerhard Heller, Department of Zoology II, University Erlangen-Nürnberg, Staudtstr. 5, D-8520 Erlangen, FRG

Z. Säugetierkunde 54 (1989) 9–21

ISSN 0044-3468

Histochemistry of complex carbohydrates in the scrotal skin of the monkey *Macaca cyclopis* (Swinhoe)

By W. Meyer and A. Tsukise

Institut für Zoologie, Tierärztliche Hochschule Hannover; Department of Veterinary Anatomy, College of Agriculture and Veterinary Medicine, Nihon University, Fujisawa

Receipt of Ms. 21. 9. 1987

Abstract

Studied the scrotal skin of the monkey, *Macaca cyclopis* (Swinhoe), by means of a series of selected histochemical methods for the detection of carbohydrates, including peroxidase-labelled lectin-diaminobenzidine procedures. The results obtained were most distinct in the two tubular gland types (apocrine glands, eccrine glands), and, to some extent, in the sebaceous glands, and the upper layers of the vital epidermis. Weak staining reactions were limited to the dermis.

The cytoplasm and free surface of the secretory cells, and the luminal secretions of the apocrine glands, and, in particular, the eccrine glands contained only very few acidic glycoproteins, including small amounts of sialic acid, but mostly neutral glycoproteins with various saccharide residues: α-D-mannose, α-D-glucose, β-D-galactose, α-D-galactose, N-acetyl-D-galactosamine in the apocrine glands; and β-D-galactose, α-D-galactose, N-acetyl-D-galactosamine, α-fucose, N-acetyl-β-D-glucosamine in the eccrine glands (superficial cells). These glands additionally exhibited small amounts of glycogen. The sebaceous glands contained glycoproteins with the following sugar residues: α-D-mannose, α-D-glucose, N-acetyl-α-D-galactosamine and sialic acid.

The secretions of the three gland types in the scrotal skin of the monkey are mixed on the surface of the scrotum, forming a mucous coat of mainly neutral glycoproteins. Their most important function may be connected with the release of volatile odorous substances after microbial degradation. The odours produced could be significant for intraspecific communication by the signalling of sexual activity. Thus, the scrotal skin of cercopithecoid species may act as a glandular organ, as hitherto assumed only for prosimians or ceboid species.

Introduction

Recent histochemical studies on the scrotal skin of different mammalian species demonstrated that the tubular apocrine glands of this specific body region have a relatively broad functional significance, and are not only concerned with thermoregulation. This is especially due to the type of secretion elaborated by these glands, particularly in relation to the mucus released on the skin surface (Tsukise and Yamada 1981; Tsukise and Meyer 1982, 1987; Tsukise et al. 1985; Meyer et al. 1986). The substances in question could be essential for the production of different odours, i.e. they would be important for intraspecific communication. In mammals, chemical signals are often involved in priming reproductive functions, and mediating sexual and social communicatory behaviour (see e.g. Mykytowicz and Goodrich 1974; Cheal 1975; Albone 1984). This is also true of primates, but only with special reference to many prosimians (Tupaiidae, Lemuridae, Lorisidae) or families of the Ceboidea (Callithricidae, Cebidae) (see e.g. Epple 1976; Schilling 1979; Zeller 1986), and is probably reflected by the high development of their rhinencephalon (Starck 1965).

The Cercopithecoidea (old world monkeys), however, are relatively devoid of specialized skin scent glands and ritualized scent-marking behaviour patterns, although olfactory investigation, including mutual investigation is very common in most species. The genitals provide a major focus of attention, in females (vaginal odour, urine) as well as

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5401-0009 $ 02.50/0

in males (Marler 1965; Gautier and Gautier 1977; Albone 1984). Information about the scrotal skin of primates other than man is generally scarce, and largely confined to prosimian groups (Wislocki 1930; Schaffer 1940; Ellis and Montagna 1959; Fiedler 1959; Starck 1969). For macaques, this is in contrast to the broad evidence available on the structure of the hairy skin and most specific body regions, including several aspects of eccrine gland function (see e.g. Lee 1960; Machida et al. 1964; Montagna et al. 1964; Im and Montagna 1965; Johnson and Elizondo 1974; Sato 1983). In this connection, and in view of the problems discussed above, it seemed appropriate to analyse the scrotal skin of a macaque species, using carbohydrate histochemical methods. Thus, this study primarily supplies a differentiation of the secretions of the three gland types present, with special reference to the tubular eccrine glands which are not found in the scrotal skin of other mammalian groups.

Materials and methods

Four adult males of the Formosa macaque, *Macaca cyclopis* (Swinhoe, 1862) (Catarrhina, Cercopithecidae), were examined in the present study. After the animals were sacrificed, skin specimens from ventrolateral parts of the scrotum were dissected out, and fixed for 48 h at room temperature in the following solutions: Bouin's solution, 10 % formalin containing 2 % calcium acetate (Leppi 1968), and 10 % formalin in 95 % ethanol (McManus and Mowry 1958). After dehydration in a series of graded ethanol concentrations, the tissue pieces were embedded in paraffin wax, and cut 6 μm. Sections were deparaffinized in xylene, rehydrated through graded ethanol concentrations and stained with the following procedures:

Haematoxylin and eosin (H-E); periodic acid-Schiff (PAS) (Spicer et al. 1967); alcian blue (AB), pH 1.0 (Lev and Spicer 1964), and AB, pH 2.5 (Pearse 1968); dialysed ironferrocyanide (DI-FCY) (Yamada 1973); AB, pH 2.5-PAS (Mowry 1963); coupled tetrazonium procedure (TZ), (Pearse 1968); and lectins labelled with horseradish peroxidase (PO) (purchased from E. Y. Laboratories, U.S.A.) – concanavalin A (Con A), peanut agglutinin (PNA), *Dolichos biflorus* agglutinin (DBA), *Ricinus communis* agglutinin-I (RCA-I), *Maclura pomifera* agglutinin (MPA), *Ulex europaeus* agglutinin-I (UEA-I), soy bean agglutinin (SBA), wheat germ agglutinin (WGA), *Griffonia simplicifolia* agglutinin-I and -II (GSA-I and -II), and *Limulus polyphemus* agglutinin (LPA) (Collard and Temmink 1974; Kiernan 1975; Yamada and Shimizu 1977, 1979; Stoward et al. 1980; Tsukise and Yamada 1981; Alroy et al. 1984). The activity of peroxidase employed for labelling was revealed by a diaminobenzidine-hydrogen peroxide system (DAB; purchased from Sigma Chemicals) (Yamada and Shimizu 1977).

The following confirmatory and control experiments were performed:

1. Enzyme digestion: α-amylase (Sigma Chemicals) 1 mg/ml in 0.1 M phosphate buffer (pH 7.0) at 37 °C for 3 h (Casselman 1969), prior to staining with PAS or PO-Con A-DAB. For the enzyme digestion experiments, two types of controls were performed: (a) some tissue sections were incubated in the buffer solution without enzyme, under identical conditions of temperature and duration; (b) other sections were kept intact without any incubation procedures.
2. Chemical modification: sulfation (Yamada and Hoshino 1972), prior to staining with AB (pH 1.0).
3. Lectin controls: the following saccharides were added at a final concentration of 0.01 M to the respective lectin solutions: α-methyl-D-mannoside for Con A, lactose for PNA, N-acetyl-D-galactosamine for DBA, galactose for RCA-I, SBA, MPA and GSA-I, L-fucose for UEA-I, N-acetyl-D-glucosamine for WGA and GSA-II, and N-acetyl-neuraminic acid for LPA.
   To detect endogenous peroxidase activity in tissues, certain control sections were reacted with DAB only.

Additionally some skin specimens were prepared for scanning electron microscopy according to Meyer and Neurand (1985). After coating with gold-palladium, the samples were viewed in a JEOL JSM-35C scanning electron microscope at 25 kV.

Results

The scrotal skin of the monkey, *Macaca cyclopis,* is only sparsely studded with hair follicles, including the relatively large sebaceous glands of the latter, and shows in close proximity apocrine and eccrine tubular glands (Figs. 1–3, 18–21). The apocrine glands

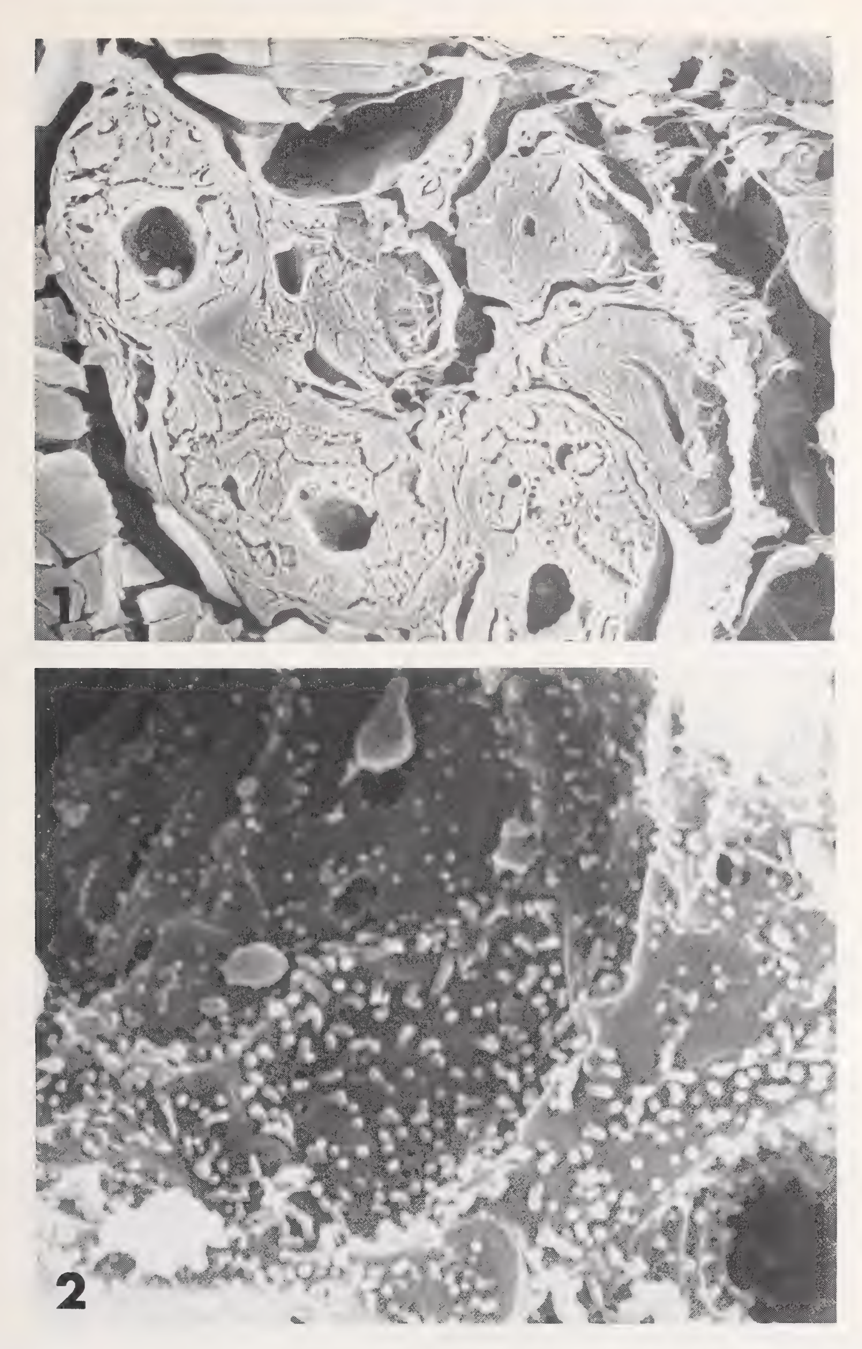


Fig. 1. SEM of tubules of eccrine glands; ×810. – *Fig. 2.* SEM of the luminal surface of superficial cells of eccrine gland; ×1440

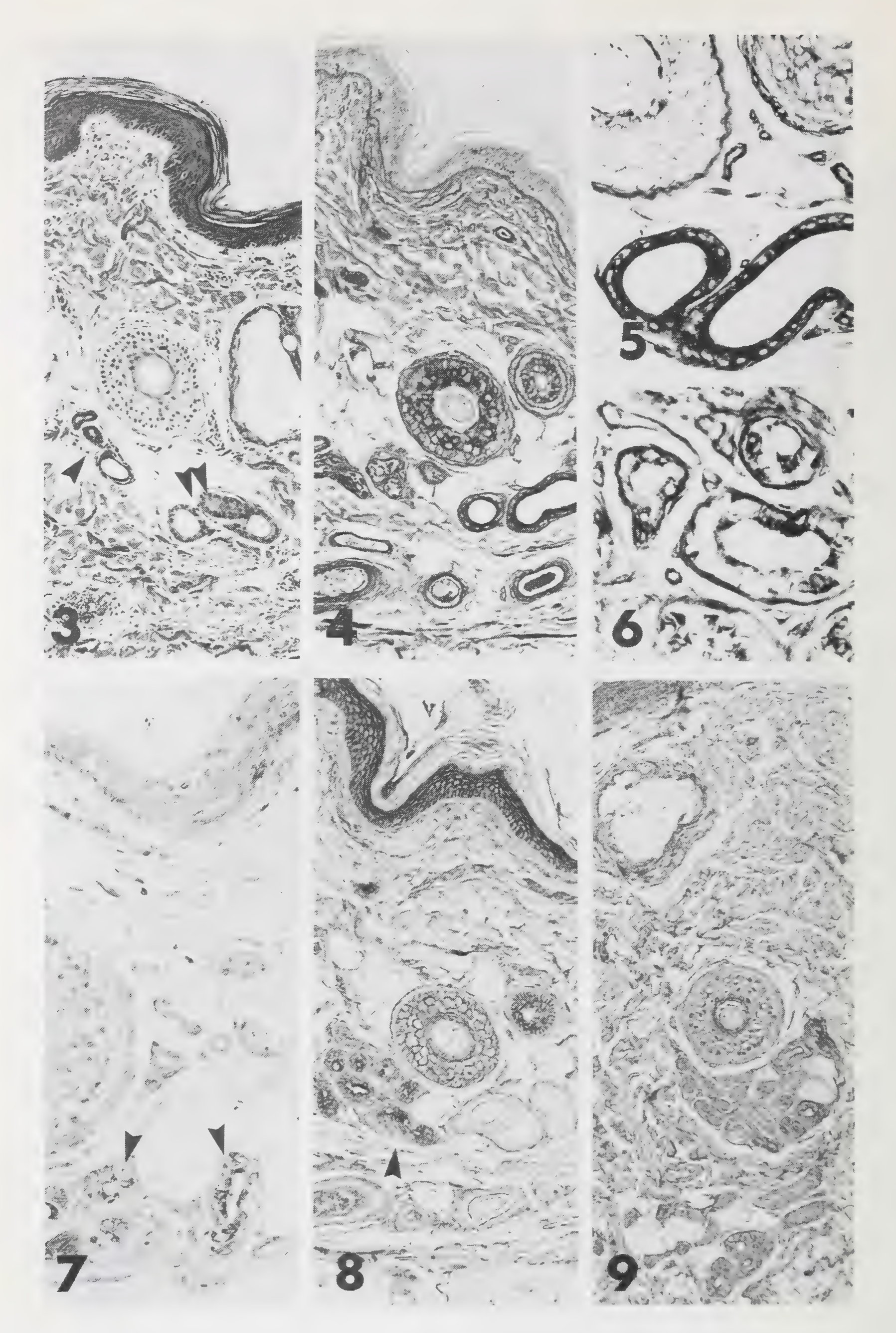


Fig. 3. General view of monkey scrotal skin with eccrine (arrow) and apocrine tubular glands (double arrow); H.E., ×90. – *Fig. 4.* as Fig. 3: PAS stained, ×90. – *Fig. 5.* apocrine gland tubules; AB (pH 2.5)-PAS, ×180. – *Fig. 6.* eccrine gland tubules; AB (pH 2.5)-PAS, ×180. – *Fig. 7.* AB (pH 2.5), with clearly positive reactions in superficial cells of eccrine glands (arrow), ×360. – *Fig. 8.* PO-WGA-DAB, clearly positive reactions only in eccrine glands (arrow), ×90. – *Fig. 9.* PO-LPA-DAB, ×90

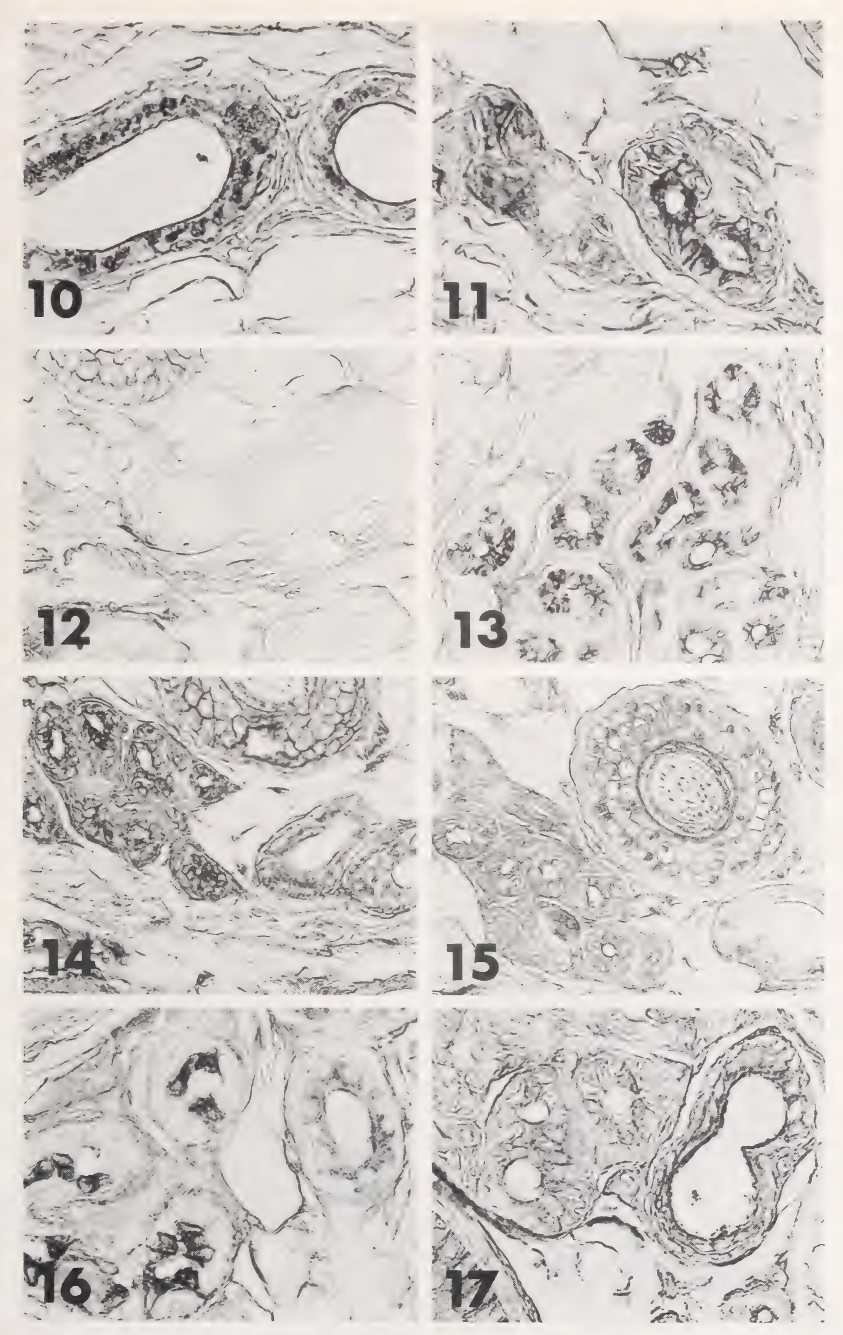


Fig. 10. PO-SBA-DAB; apocrine gland tubules, ×360. – *Fig. 11.* PO-SBA-DAB; eccrine gland tubules, ×360. – *Fig. 12.* PO-UEA-I-DAB; apocrine gland tubules, ×180. – *Fig. 13.* PO-UEA-I-DAB; eccrine gland tubules, ×180. – *Fig. 14.* PO-RCA-I-DAB; eccrine and apocrine gland tubules (right), ×180. – *Fig. 15.* PO-DBA-DAB; eccrine and apocrine gland tubules (right), ×180. – *Fig. 16.* PO-GSA-I-DAB; strong reactions only in superficial cells of eccrine glands, ×360. – *Fig. 17.* PO-MPA-DAB; stronger staining of the luminal surface of apocrine glands, ×360



Fig. 18. PO-Con A-DAB; ×90. – *Fig. 19.* PO-PNA-DAB; strong staining of epidermal intercellular substances, positive reactions also in sebaceous gland cells (below), ×180. – *Fig. 20.* PO-RCA-I-DAB; distinct reaction of intercellular substances, ×180. – *Fig. 21.* PO-DBA-DAB; clearly positive reactions especially in peripheral cells of sebaceous glands, ×180

exhibit a comparatively flat secretory epithelium with only slight apocrine protrusions at the cell apices. The eccrine glands are composed of the typical pattern of superficial and basal secretory cells (dark and clear cells), and the luminal surface of the cells is provided with a sparse coat of short microvilli (Fig. 2). The epidermis is normally structured, with several layers of the stratum spinosum, one continuous layer of the stratum granulosum, and a few lamellae of the stratum corneum. The dermis is relatively thin and includes a densely interwoven meshwork of fine and medium-sized collagen fibre bundles.

The selected histochemical methods used in the present study demonstrated a variety of distribution patterns of complex carbohydrates. The results obtained in the different skin structures are summarized in Tables 1 (skin layers), 2 (apocrine glands and eccrine glands) and 3 (sebaceous glands). The strongest reactions were observed in the apocrine glands, the eccrine glands, and, to some extent, in the sebaceous glands, less intense stainings were generally limited to the skin layers, especially the dermis.

PAS, AB (pH 2.5), DI-FCY and AB (pH 2.5)-PAS staining resulted in positive colourations of moderate to strong intensities of the secretory cells and luminal secretions of both tubular gland types, but particularly in the apocrine glands (Figs. 4, 5). In the secretory epithelium of the eccrine glands strong reactions were confined to the superficial cells (dark cells) (Figs. 6, 7). Clearly positive reactions for these staining procedures were also visible in the sebum of the sebaceous glands, the inner surface of the blood vessels, and the connective tissue elements of the dermis and subcutis. Digestion with α-amylase failed to notably alter the PAS staining of all skin structures investigated, except for the superficial cells of the eccrine glands. The AB (pH 1.0) reaction intensity was significantly increased by prior sulfation. The tetrazonium staining procedure coloured moderately or strongly nearly every skin structure, particularly the secretory cells of the apocrine glands and the superficial cells of the eccrine glands.

The reactions of PO-labelled lectins with the structures of the monkey scrotal skin exhibited somewhat different staining patterns, depending on the lectins employed. Markedly and strongly positive reactions were confined to the secretory epithelium

Table 1. **Carbohydrate histochemical reactions in the skin layers of the monkey scrotum**

Reactions	Epidermis				Dermis		Subcutis
	Stratum corneum	Stratum granulosum	Stratum spinosum	Stratum basale	Connective tissue	Blood vessels	Connective tissue
PAS	–	+	+	(+)/+	+/++	++/+++	+
AB (pH 1.0)	–	(+)	(+)	(+)	(+)/+	(+)	(+)/+
AB (pH 2.5)	(+)/+	++	++	+/++	+/++	+/++	+
AB (pH 2.5)-PAS	–	+	+	(+)/+	+/++	++/+++	+
AMYL-PAS	–	+	+	(+)/+	+/++	++/+++	+
SUL-AB (pH 1.0)	+	+/++	+	+	++/+++	+/++	+/+++
TZ	++/+++	++/+++	++	+	++	+/++	++
PO-Con A-DAB	(+)	++/+++	++/+++	+	+/++	++	+/++
PO-PNA-DAB	(+)/+	++/+++	++	+	+/++	+	+/++
PO-DBA-DAB	(+)/+	++	+/++	+	+	+/++	+
PO-RCA-I-DAB	(+)/+	++/+++	++	+	++	+	++
PO- MPA-DAB	(+)/+	++	+	+	+	+	++
PO-UEA-I-DAB	(+)	++	+/++	+	+	(+)	+
PO-SBA-DAB	+	++	++	+	+	+	+
PO-WGA-DAB	+	++/+++	+/++	+	+	+	+
PO-GSA-I-DAB	+	+/++	+	(+)/+	+/++	+	+/++
PO-GSA-II-DAB	+/++	(+)/+	(+)/+	(+)	+	+	+/++
PO-LPA-DAB	+	++	++	++	+/++	+/++	+/++

Reaction intensities (for all Tables): – = no reaction visible, (+) = very weak, + = weak, ++ = moderate, +++ = strong

Table 2. **Carbohydrate histochemical reactions in the apocrine and eccrine glands of the monkey scrotum**

Reactions	Apocrine glands				Eccrine glands			
	Secretory cells	Luminal secretion	Excretory durct cells	Myoepi-thelial cells	Secretory cells		Luminal secretion	Excretory duct
					Superficial	Basal		
PAS	++/+++	++	++	(+)	++	(+)/+	(+)	+
AB (pH 1.0)	++	+	+	(+)	(+)/+	–	(+)	(+)
AB (pH 2.5)	++/+++	++	+/++	+	++/+++	(+)	+	+
AB (pH 2.5)-PAS	+++	++	++	+	++	(+)/+	+	+
AMYL-PAS	++/+++	++	++	(+)	+/++	(+)/+	(+)	(+)
SUL-AB (pH 1.0)	++/+++	+	+	+	+	(+)	+	+
TZ	+++	++	++/+++	++	++/+++	+	++	+/++
PO-Con A-DAB	+/++	(+)	(+)	(+)/+	++	+	+	+
PO-PNA-DAB	+	(+)	(+)	(+)	+/++	(+)	(+)	(+)
PO-DBA-DAB	(+)	(+)	(+)	(+)	+/++	(+)	(+)	(+)
PO-RCA-I-DAB	++	(+)	(+)	(+)	++/+++	(+)	+	+
PO-MPA-DAB	+/++	(+)	(+)	(+)	++	(+)	(+)	(+)
PO-UEA-I-DAB	–	–	–	–	++/+++	–	(+)	–
PO-SBA-DAB	++	+	(+)	(+)	++/+++	(+)	(+)	+
PO-WGA-DAB	(+)	(+)	(+)	–	++/+++	(+)	(+)	(+)
PO-GSA-I-DAB	+	(+)	(+)	–	+++	(+)	+	(+)
PO-GSA-II-DAB	–	–	–	–	(+)	–	–	–
PO-LPA-DAB	(+)	(+)	(+)	–	+	(+)	(+)	(+)

Table 3. **Carbohydrate histochemical reactions in the sebaceous glands of the monkey scrotum**

Reactions	Sebaceous glands			
	Peripheral cells	Central cells	Excretory duct cells	Secretion
PAS	+/++	+	+	+/++
AB (pH 1.0)	(+)/+	–	–	(+)/+
AB (pH 2.5)	+	(+)/+	(+)/+	(+)/+
AB (pH 2.5)-PAS	+/++	+	+	+++
AMYL-PAS	+/++	+	+	+/++
SUL-AB (pH 1.0)	+/++	+	+	++
TZ	+/++	+	+	+
PO-Con A-DAB	++/+++	++	++	++
PO-PNA-DAB	++	+/++	+	++
PO-DBA-DAB	++/+++	+/++	+	++
PO-RCA-I-DAB	++	+/++	+	++
PO-MPA-DAB	++	++	+	++
PO-UEA-I-DAB	+/++	+	+	++
PO-SBA-DAB	+	(+)/+	(+)/+	+/++
PO-WGA-DAB	+/++	++	+	++/+++
PO-GSA-I-DAB	+	(+)/+	+	++
PO-GSA-II-DAB	(+)/+	+	(+)	++
PO-LPA-DAB	+/++	++	+	++

(superficial cells) of the eccrine glands (RCA-I, UEA-I, SBA, WGA, GSA-I) (Figs. 8, 11, 13, 14, 16), the sebaceous glands (Con A, DBA) (Figs. 18, 21) and their secretion (WGA, LPA) as well as the stratum granulosum and stratum spinosum of the epidermis. In the latter, the strong reaction stainings could only be observed in the intercellular substances (Con A, PNA, RCA-I, WGA) (Figs. 8, 18–20). Of all the lectins used, the PO-LPA staining was generally weak in most skin structures, including, for example, the two tubular gland types and their secretions. In the sebaceous glands, however, a weak to

moderate intensity for PO-LPA was found in the cells, the sebum and the interlobular and peripheral connective tissue. In the control procedures for the PO-labelled lectin staining, the addition of particular saccharides to the PO-lectin solutions diminished greatly, or abolished the intensity of the lectin reaction in all the skin structures tested.

Discussion

The results obtained in the course of this histochemical study have demonstrated that glycoconjugates, such as neutral and acidic glycoproteins, are clearly present in the scrotal skin of the monkey, *Macaca cyclopis* (Swinhoe). The well established properties of the PAS, AB (pH 1.0), AB (pH 2.5), AB (pH 2.5)-PAS, and several PO-lectin stainings indicate that the distribution patterns of the complex carbohydrates observed, to some extent, are similar to those shown in the scrotal skin of other mammals (Tsukise and Yamada 1981; Tsukise and Meyer 1982, 1987; Tsukise et al. 1985; Meyer et al. 1986). Differences, however, are evident when the tubular glands and their secretions are compared.

The reaction stainings as visible from the skin layers were most remarkable in the epidermis, where the glycoconjugates in the cell walls and, particularly, in the intercellular substances exhibited the presence of the following sugar residues: α-D-glucose, α-D-mannose, β-D-galactose, N-acetyl-α-glucosamine. These findings are in general accordance with observations from the human skin (Holt et al. 1979; Nemanic and Elias 1979; Reano et al. 1982; Ookusa et al. 1983; Schaumburg-Lever et al. 1984), or mammals with a sparse hair coat like the domestic pig (Tsukise and Meyer 1983; Meyer 1986). The intercellular substances include glycoproteins for cell adhesion (Hashimoto et al. 1974; Rauvala et al. 1981) or glycolipids to prevent epidermal water loss (Wertz and Downing 1982; Odland 1983; Meyer 1986). Thus, the large amounts of glycoconjugates among the upper layers of the vital epidermis of scrotal skin seem to compensate for the reduced protective properties of the normally sparse hair coat of the scrotum (see also Meyer 1986). The observations on residue distribution and staining intensity in fibre bundles of the dermis correspond to that demonstrated in the scrotal skin of other mammals (Tsukise and Yamada 1981; Tsukise et al. 1985; Tsukise and Meyer 1987).

As already emphasized in the introduction, the most interesting aspects of the macaque scrotal skin may be connected with the secretions elaborated by the three different gland types found. Carbohydrate histochemical differentiation showed that the cytoplasm, the free surface of the secretory cells, and the luminal secretion of the apocrine glands and, in particular, the eccrine glands contained mostly neutral but only very few acidic glycoproteins, including small amounts of sialic acid. The results of the PO-lectin-DAB procedures indicate that the following saccharide residues are predominant in the neutral glycoproteins present: α-D-mannose, α-D-glucose, β-D-galactose, α-D-galactose, N-acetyl-D-galactosamine in the apocrine glands; and, somewhat different, β-D-galactose, α-D-galactose, N-acetyl-D-galactosamine, α-fucose, N-acetyl-β-D-glucosamine in the eccrine glands (superficial cells); and α-D-mannose, α-D-glucose, N-acetyl-α-D-galactosamine, sialic acid in the sebaceous glands (for residue demonstration see e.g. Kiernan 1975; Yamada and Shimizu 1977; Stoward et al. 1980; Tsukise and Yamada 1981; Alroy et al. 1984).

The histochemical characteristics as obtained for the apocrine glands are in keeping with findings described for this gland type in the scrotal skin of other species (Tsukise and Yamada 1981; Tsukise and Meyer 1982, 1987; Tsukise et al. 1985; Meyer et al. 1986), although it was quite obvious that in the monkey the amounts released were distinctly smaller. The eccrine glands, on the contrary, seemed to be more active, and their spectrum of saccharide residues mainly agrees with that observable in human eccrine glands of the common integument (see e.g. Ookusa et al. 1983; Schaumburg-Lever et al. 1984), or

that found in the eccrine glands of the pig snout (Tsukise et al. 1983). Our results also confirm the view of Constantine and Mowry (1966) assuming that this gland type in humans contains acidic carbohydrates only with carboxyl groups and only a few sialic acid residues. In addition, the eccrine glands in the monkey scrotal skin exhibited small amounts of glycogen, a feature common also to these glands in the human skin or the pig snout, and probably related to high energy demands during sweating or secretion production, respectively (Smith and Dobson 1966; Ellis 1968; Tsukise et al. 1983).

The secretions of the two tubular gland types are finally released onto the skin surface. Here, their functions are manifold, and can only be evaluated in view of the fact that they soon become parts of a mixture of different substances when those glycoconjugates are included which are elaborated by the sebaceous glands (see also Tsukise and Meyer 1987). As could be expected from the generally neutral pH of the eccrine gland secretions in monkeys and man (Sato 1983), the acidity of this mixture is rather low, so that the suppression of pathogenic microorganisms may be of minor importance, as should be evaporative cooling because of the relatively small scrotal evaporative area.

The most important function of the mucous coat of neutral glycoproteins on the scrotum of monkeys may be related to volatile odorous substances as released by microbial degradation (for literature see e.g. Albone 1984). The odours produced could be significant for intraspecific communication by the signalling of sexual activity. Monkeys and apes may generally make more use of olfaction than is at present appreciated, and, as visible from their sensitive discrimination between edible and non-edible food or objects, macaques have highly developed olfactory senses (Cole 1963; Marley 1965). The relation to sexual life may be closely connected with changes in scrotal gland structure and secretory rates in times of sexual activity or inactivity due to androgenic influences, as demonstrated in humans (Wilson and Walker 1969; Ebling 1980; Kutenn et al. 1980). In macaques, for example, the blood level of testosterone increases two-fold in males upon interaction with sexually active females (Rose et al. 1972). Thus, the scrotal skin is probably a glandular organ, not only in prosimians (Fiedler 1959) or Ceboidea (Starck 1969), but, to a certain degree, also in the Cercopithecoidea.

Zusammenfassung

Die Histochemie komplexer Kohlenhydrate in der Skrotalhaut des Formosa-Makaken, Macaca cyclopis (Swinhoe)

Die Skrotalhaut des Formosa-Makaken, *Macaca cyclopis* (Swinhoe), wurde mit einer Reihe von histochemischen Methoden zur Darstellung von Kohlenhydraten untersucht, wobei auch Peroxidase-gekoppelte Lektine zur Anwendung kamen. Die kräftigsten Reaktionen waren in den zwei tubulären Drüsentypen (apokrine Drüsen, ekkrine Drüsen) sowie z.T. in den Talgdrüsen und den oberen Lagen der vitalen Epidermis zu entdecken. Schwächere Anfärbungen beschränkten sich auf die Dermis.

Das Cytoplasma und die freie Oberfläche der sekretorischen Zellen sowie das Sekret im Lumen der apokrinen Drüsen und, im besonderen, der ekkrinen Drüsen enthielt zwar nur wenig saure Glykoproteine, einschließlich geringer Mengen an Sialinsäuren, dafür aber deutlich mehr neutrale Glykoproteine mit verschiedenen Zuckerresten: α-D-Mannose, α-D-Glukose, β-D-Galaktose, α-D-Galaktose, N-Azetyl-D-Galaktosamin in den apokrinen Drüsen; und β-D-Galaktose, α-D-Galaktose, N-Azetyl-β-D-Glukosamin in den ekkrinen Drüsen (dunkle Zellen). Diese Drüsen wiesen auch geringe Mengen an Glykogen auf. Die Talgdrüsen besaßen Glykoproteine mit folgenden Zuckerresten: α-D-Mannose, α-D-Glukose,N-Azetyl-α-D-Galaktosamin und Sialinsäuren.

Die Sekrete der drei Drüsentypen in der Skrotalhaut des Formosa-Makaken bilden als Sekretmischung auf der Oberfläche des Skrotums eine dünne muköse Schicht aus zumeist neutralen Glykoproteinen. Ihre wichtigste Funktion könnte die durch mikrobielle Zersetzung hervorgerufene Freisetzung von flüchtigen Geruchssubstanzen sein. Die so produzierten Düfte haben im Rahmen der innerartlichen Kommunikation vielleicht die Aufgabe, sexuelle Aktivität zu signalisieren. Die Skrotalhaut der Cercopithecoidea kann daher, ebenso wie bei Prosimiern und Ceboidea, eventuell als Drüsenorgan verstanden werden.

Literature

Albone, E. S. (1984): Mammalian semiochemistry. The investigation of chemical signals between mammals. Chichester, New York, Brisbane, Toronto, Singapore: J. Wiley.

Alroy, J.; Ucci, A. A.; Pereira, M. E. A. (1984): Lectins: histochemical probes for specific carbohydrate residues. In: Advances in immunohistochemistry. Ed. by R. A. de Lellis. New York: Masson. 67–88.

Casselman, W. G. B. (1969): Histochemical technique. London: Methuen.

Cheal, M. (1975): Social olfaction: a review of the ontogeny of olfactory influences on vertebrate behavior. Behav. Biol. **15**, 1–25.

Cole, J. (1963): *Macaca nemestrina* studied in captivity. Symp. Zool. Soc. London **10**, 105–114.

Collard, J. G.; Temmink, J. H. M. (1974): Binding and cytochemical detection of cell-bound concanavalin A. Expl. Cell Res. **86**, 81–86.

Constantine, V. S.; Mowry, R. W. (1966): Histochemical demonstration of sialomucin in human eccrine sweat glands. J. invest. Dermatol. **46**, 536–541.

Ebling, F. J. (1980): Hormonal steroids in dermatology. In: Percutaneous absorption of steroids. Ed. by P. Mauvais-Jarvis; C. F. H. Vickers; J. Wepierre. London, New York, Toronto, Sydney, San Francisco: Academic Press. 139–147.

Ellis, R. A. (1968): Eccrine sweat glands: electron microscopy, cytochemistry and anatomy. In: Handbuch der Haut- und Geschlechtskrankheiten, Ergänzungswerk I/1. Ed. by J. Jadassohn. Berlin: Springer. 224–266.

Ellis, R. A.; Montagna, W. (1959): Comparative histochemistry of the sweat glands of primates. J. Histochem. Cytochem. **7**, 308.

Epple, G. (1976): Chemical communication and reproductive processes in non-human primates. In: Mammalian olfaction, reproductive processes, and behavior. Ed. by R. Doty. New York: Academic Press. 257–282.

Fiedler, W. (1959): Über Differenzierungen der Scrotalhaut von *Perodicticus potto* (Müller 1766) im Vergleich mit anderen Prosimiae. Acta anat. **37**, 80–105.

Gautier, J. P.; Gautier, A. (1977): Communication in old world monkeys. In: How animals communicate. Ed. by T. A. Seboek. Bloomington: Indiana Univ. Press. 890–964.

Hashimoto, K.; King, L. E.; Yamanishi, Y.; Beachey, E. H.; Maeyens, E. (1974): Identification of the substance binding pemphigus antibody and concanavalin A in the skin. J. invest. Dermatol. **62**, 423–435.

Holt, P. J. A.; Hill-Anglin, J.; Nordquist, R. E. (1979): Localization of specific carbohydrate configurations in human skin using fluorescein-labelled lectins. Brit. J. Dermatol. **100**, 237–245.

Im, M. J. C.; Montagna, W. (1965): The skin of primates. XXVI. Specific and nonspecific phosphatases in the skin of the rhesus monkey. Am. J. Phys. Anthrop. **23**, 131–134.

Johnson, G. S.; Elizondo, R. S. (1974): Eccrine sweat gland in *Macaca mulatta:* physiology, histochemistry, and distribution. J. appl. Physiol. **37**, 814–820.

Kiernan, J. A. (1975): Localization of α-D-glucosyl and α-D-mannosyl groups of mucosubstances with concanavalin A and horseradish peroxidase. Histochemistry **44**, 39–45.

Kutenn, F.; Mowszowicz, I.; Mauvais-Jarvis, P. (1980): Androgen metabolism in human skin. In: Percutaneous absorption of steroids. Ed. by P. Mauvais-Jarvis; C. F. H. Vickers; J. Wepierre. London, New York, Toronto, Sydney, San Francisco: Academic Press. 99–121.

Lee, M. M. C. (1960): Histology and histochemistry of human eccrine sweat glands, with special reference to their defense mechanisms. Anat. Rec. **136**, 97–105.

Leppi, T. J. (1968): Morphochemical analysis of mucous cells in the skin and slime glands of hagfisches. Histochemie **15**, 68–78.

Lev, R.; Spicer, S. S. (1964): Specific staining of sulphate groups with Alcian Blue at low pH. J. Histochem. Cytochem. **12**, 309.

Machida, H.; Perkins, E.; Montagna, W. (1964): The skin of primates. XXIII. A comparative study of the skin of the green monkey *(Cercopithecus aethiops)* and the Sykes' monkey *(Cercopithecus mitis).* Am. J. Phys. Anthrop. **22**, 453–466.

Marler, P. (1965): Communication in monkeys and apes. In: Primate behavior. Ed. by J. Devore. New York, Chicago, San Francisco, Toronto, London: Holt, Rinehart and Winston. 544–584.

McManus, J. F. A.; Mowry, R. W. (1958): Effects of fixation on carbohydrate histochemistry. J. Histochem. Cytochem. **6**, 309–316.

Meyer, W. (1986): Die Haut des Schweines. Hannover: Schlüter.

Meyer, W.; Neurand, K. (1985): Comparative SEM of the skin of domestic mammals. In: Functional morphology in vertebrates (Fortschr. Zool., Vol. 30). Ed. by H. R. Duncker, G. Fleischer. Stuttgart, New York: G. Fischer. 479–481.

Meyer, W.; Tsukise, A.; Neurand, K. (1986): Histochemical observations on the apocrine glands of the scrotal skin of the cat and dog. Morph. Jb. **133**, 163–173.

Montagna, W.; Yun, J. S.; Machida, H. (1964): The skin of primates. XVIII. The skin of the rhesus monkey *(Macaca mulatta).* Am. J. Phys. Anthrop. **22**, 307–320.

Mowry, R. W. (1963): The special value of methods that colour with acidic and hydroxyl groups in the histochemical study of mucins. With revised directions for the colloidal iron stain, the use of Alcian Blue 8GX and their combination with the periodic acid-Schiff reaction. Ann. N. Y. Acad. Sci. **106**, 402–423.
Mykytowycz, R.; Goodrich, B. S. (1974): Skin glands as organs of communication in mammals. J. invest. Dermatol. **62**, 124–131.
Nemanic, M. K.; Elias, P. M. (1979): Localization and identification of sugars in mammalian epidermis. J. Cell Biol. **83**, 46a.
Odland, G. F. (1983): Structure of skin. In: Biochemistry and physiology of the skin. Vol. 1. Ed. by L. A. Goldsmith. New York, Oxford: Oxford Univ. Press. 3–63.
Ookusa, Y.; Takata, K.; Nagashima, M.; Hirano, H. (1983): Distribution of glycoconjugates in normal human skin using biotinyl lectins and avidin-horseradish peroxidase. Histochemistry **79**, 1–7.
Pearse, A. G. E. (1968): Histochemistry. Theoretical and applied. Vol. 1. London: Churchill.
Rauvala, H.; Carter, W. G.; Hakomori, S. (1981): Studies on cell adhesion and recognition. 1. Extent and specificity of cell adhesion triggered by carbohydrate-reactive proteins (glycosidases and lectins) and by fibronectin. J. Cell Biol. **88**, 127–137.
Reano, A.; Faure, M.; Jacques, Y.; Reichert, U.; Schaefer, H.; Thivolet, J. (1982): Lectins as markers of human epidermal cell differentiation. Differentiation **22**, 205–210.
Rose, R. M.; Gordon, T. P.; Bernstein, I. S. (1972): Plasma testosterone levels in the male rhesus: influence of sexual and social stimuli. Science **178**, 643–645.
Sato, K. (1983): The physiology and pharmacology of the eccrine sweat gland. In: Biochemistry and physiology of the skin. Vol. 1. Ed. by L. A. Goldsmith. New York, Oxford: Oxford Univ. Press. 596–641.
Schaffer, J. (1940): Die Hautdrüsenorgane der Säugetiere. Berlin, Wien: Urban und Schwarzenberg.
Schaumburg-Lever, G.; Alroy, J.; Ucci, A.; Lever, W. F. (1984): Distribution of carbohydrate residues in normal skin. Arch. Dermatol. Res. **276**, 216–223.
Schilling, A. (1979): Olfactory communication in prosimians. In: The study of prosimian behavior. Ed. by G. A. Doyle; R. D. Martin. New York, San Francisco, London: Academic Press. 461–542.
Smith, A. A.; Dobson, R. L. (1966): Sweating and glycogenolysis in the palmar eccrine sweat glands of the rhesus monkey. J. invest. Dermatol. **47**, 313–316.
Spicer, S. S.; Horn, R. G.; Leppi, T. J. (1967): Histochemistry of connective tissue mucopolysaccharides. In: The connective tissue. Ed. by B. M. Wagner; D. E. Smith. Baltimore: Williams and Wilkins. 251–303.
Starck, D. (1965): Die Neencephalisation (Die Evolution zum Menschenhirn). In: Menschliche Abstammungslehre, Fortschritte der Anthropogenie 1863–1964. Ed. by G. Heberer. Stuttgart: G. Fischer. 103–144.
— (1969): Die circumgenitalen Drüsenorgane von *Callithrix (Cebuella) pygmaea* (Spix 1823). (Über Parallelbildungen bei Primaten, ein Beitrag zur Polyphyliefrage). Zool. Garten NF **36**, 312–326.
Stoward, P. J.; Spicer, S. S.; Miller, R. L. (1980): Histochemical reactivity for peanut lectin-horseradish peroxidase conjugate. J. Histochem. Cytochem. **28**, 979–990.
Tsukise, A.; Meyer, W. (1982): Histochemistry of complex carbohydrates in the apocrine glands of the scrotal skin of the goat. Zbl. Vet. Med. **A29**, 688–693.
— — (1983): Histochemistry of complex carbohydrates in the hairy skin of the domestic pig. Histochem. J. **15**, 845–860.
— — (1987): Histochemical analysis of carbohydrates in the scrotal skin of the horse, with special reference to glandular appendages. Zool. Anz. (in press).
Tsukise, A.; Yamada, K. (1981): The histochemistry of complex carbohydrates in the scrotum of the boar. Histochemistry **72**, 511–521.
Tsukise, A.; Meyer, W.; Ikeda, T. (1985): Carbohydrate histochemical investigation in the scrotal skin of the common American opossum (*Didelphis marsupialis* L.). Cell. Mol. Biol. **31**, 357–364.
Tsukise, A.; Meyer, W.; Schwarz, R. (1983): Histochemistry of complex carbohydrates in the skin of the pig snout, with special reference to eccrine glands. Acta anat. **115**, 141–150.
Wertz, P. W.; Downing, D. T. (1982): Glycolipids in mammalian epidermis: structure and function in the water barrier. Science **217**, 1261–1262.
Wilson, J. D.; Walker, J. D. (1969): The conversion of testosterone to 5α-androstan-17β-ol-3-one (dihydrotestosterone) by skin slices of man. J. clin. Invest. **48**, 371–378.
Wislocki, G. B. (1930): A study of scent glands in the marmosets, especially *Oedipomidas geoffroyi*. J. Mammalogy **11**, 475–483.
Yamada, K. (1973): The effect of digestion with Streptomyces hyaluronidase upon certain histochemical reactions of hyaluronic acid-containing tissues. J. Histochem. Cytochem. **21**, 794–803.
Yamada, K.; Hoshino, M. (1972): Morphochemical analysis of epithelial mucosubstances in the gall bladder of the fowl *(Galluc domesticus)*. Histochemie **29**, 120–128.

YAMADA, K.; SHIMIZU, S. (1977): The histochemistry of galactose residues of complex carbohydrates as studied by peroxidase-labelled *Ricinus communis* agglutinin. Histochemistry **53**, 143–156.
— — (1979): The use of peroxidase-labelled *Limulus polyphemus* agglutinin for the histochemistry of sialic acid-containing glycoproteins in light microscopy. Histochem. J. **11**, 457–471.
ZELLER, U. (1986): Die Gulardrüse von *Propithecus* (Indriidae, Primates). Z. Säugetierkunde **51**, 1–15.

Authors' addresses: Priv.-Doz. Dr. WILFRIED MEYER, Institut für Zoologie, Tierärztliche Hochschule Hannover, Bischofsholer Damm 15, D-3000 Hannover 1, FRG; Prof. Dr. AZUMA TSUKISE, Department of Veterinary Anatomy, College of Agriculture and Veterinary Medicine, Nihon University, 1866 Kameino, Fujisawa, Kanagawa, Japan

Z. Säugetierkunde 54 (1989) 22–30

ISSN 0044-3468

A field study on seasonal changes in the circadian activity of rabbits

By J. Marijke Wallage-Drees

Department of Population Biology, University of Leiden, The Netherlands

Receipt of Ms. 3. 8. 1987

Abstract

Investigated the circadian activity of wild rabbits during the year. Wild rabbits are more nocturnal than their domestic relatives. Their emergence and disappearance times do not vary with the time of sunset and sunrise, but stay about the same during the whole year. When activity is defined as the presence above ground, then wild rabbits show one activity period with irregular fluctuations during the night. When comparing the average periods spent above ground by individuals there appear large differences between the activity during November to February and the rest of the year. Reasons for this are discussed. The highest percentage of the population above ground at one time during these winter months is lower than in the rest of the year. One should take this into account when trying to assess population size by sight counts.

Introduction

The rabbit is a prominent inhabitant of the coastal sand dunes of The Netherlands. Despite being of Mediterranean origin (Feen 1963; Zeuner 1963) it thrives at this latitude.

There are no published data on the circadian activity rhythm in wild rabbits under natural conditions at our latitude as there are from New Zealand (Gibb et al. 1978) and Australia (Mykytowycz and Rowley 1958; Myers and Poole 1961). First impressions (Southern 1940) indicate a much lower level of activity in western Europe.

Sight counts are generally used to assess the trend and size of the fluctuations in rabbit populations. Knowledge on the activity rhythm of rabbits is necessary when trying to assess population fluctuations from sight counts. Crucial aspects are: at what time of the day can one expect the highest and/or least variable proportion above ground. So this paper has two objectives: to describe the circadian rhythm and its seasonal change in a temperate climate and to give information that is useful in the interpretation of sight counts.

Material and method

The study site covered a 1.4 ha area within the reserve 'Het Noord-Hollands Duinreservaat', about 15 km northwest of Amsterdam (52.35° N; 4.37° E). Rabbits were caught in baited live-traps and earmarked. From September 1979, when a large part of the population (36 out of 41) was earmarked, monthly population size was assessed by constructing live-calendars from sightings and recaptures. Because it took some time to capture and tag the young, population size could not be calculated in all months. This accounts for the absence of data for May, June, July and August in table 1 and 2 and in figure 4. The population's area was confined on two sides by canals and on the third by a field of high grass not used by the rabbits.

Observations were recorded over 24 hours, once a month from August 1979 till April 1982. They were made from a pit with a shelter behind and above. From there about 70 % of the (hilly) area could be covered. The unseen part had the same type of vegetation. Therefore, to relate counts to total population size above ground, counts are multiplied by 100/70. There were always 2 observers, who were changed every three hours. Every 15 min it was noted which rabbits were visible. In all calculations the first observation after changing the observers was substituted by the average of the

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5401-0022 $ 02.50/0

immediately previous and subsequent observation. At dark a red spotlight was used. The rabbits' eyes, and earmarks, lighted up in the beam. As a result of the insensitivity of their retina for this long wave stimulation (NUBOER 1971) the rabbits were not disturbed by this red illumination.

One use of activity rhythm data is to aid interpretation of sight counts. The Ministry of Agriculture, Fisheries and Food (England and Wales) has long experience in conducting rabbit counts. Counts are taken during several consecutive days at dawn and dusk along transects (TITTENSOR et al. 1978). As an index of population size the maximum count is taken. The average is a less reliable measure as it is influenced strongly by incidental low values caused by disturbances (pers. comm. A. M. TITTENSOR). The index is adopted in this study.

In this article the word 'activity' means any presence above ground.

Results

Timing of start and end of activity

Figure 1 shows the times of the start and end of activity within the population. Activity is arbitrarily said to begin at the start of the first half hour in which at least 2 percent of the total activity of that day occurred and to cease at the end of the last half hour in which at least two percent of the total activity of that day occurred. For an example see Fig. 2.

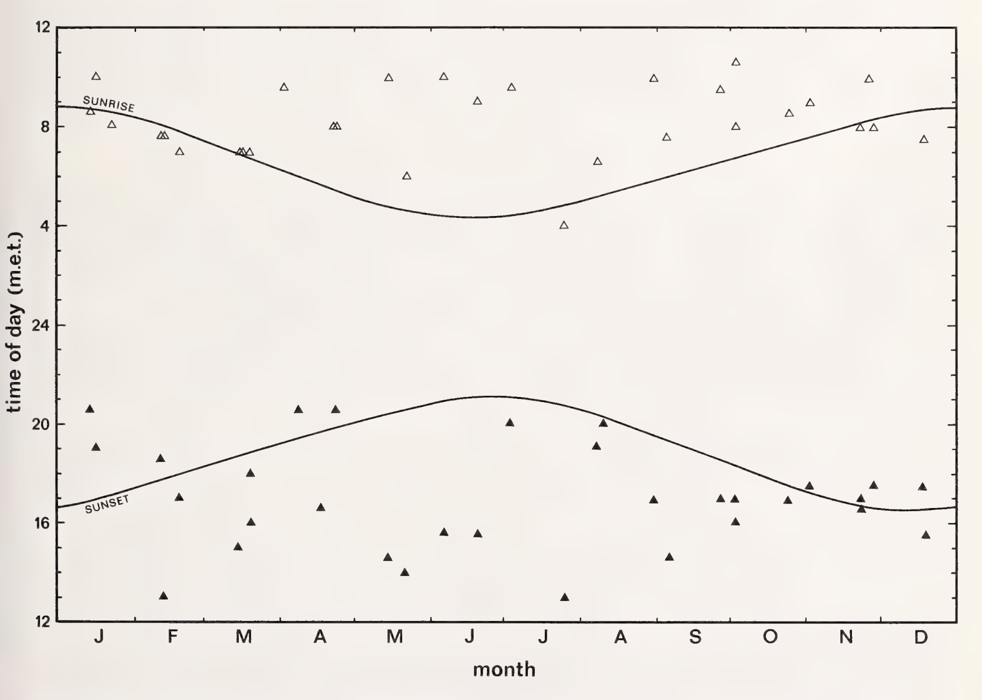


Fig. 1. Times of emergence (▲) and disappearance (△). Times of sunset and sunrise are indicated

Sometimes, in the winter, there were periods during the night with no rabbit above ground. These periods could not be taken into account in Fig. 1, but are included in calculations in the tables and Figs. 2 and 3.

In the same way, incidental activity during the daytime separated by at least an hour from the main activity period, is not taken into account in Fig. 1.

A close relation between activity period and times of sunset or sunrise may have been expected. HOF et al. (1963) showed that in domestic rabbits the time of light-on (sunrise) is

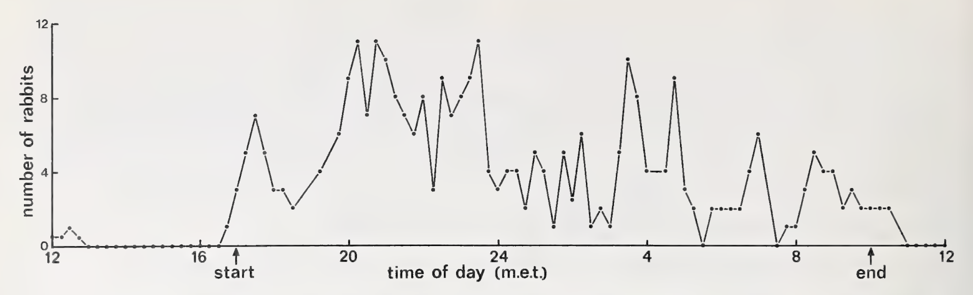


Fig. 2. Activity pattern (number of rabbits/30 min) on 2 October 1979. Arrows indicate times of emergence and disappearance as they are calculated in this paper

the trigger that determines emergence time. So one would expect a correlation between time of sunrise and start of activity. In this study, however, correlation coefficients are not significant (sunrise-start of activity, $r = 0.08$, $n = 32$, $p = 0.3$; and sunrise-end of activity, $r = -0.06$, $n = 31$, $p = 0.4$).

Holley and Greenwood (1984), studying the brown hare found the absence of this relationship to be characteristic of the summer. So I calculated sunrise-start of activity for autumn, winter and spring together, but did not find a significant correlation (Sept.–April, $r = -0.07$, $n = 23$, $p = 0.4$). There are large, apparently irregular fluctuations. The mean times of emergence and disappearance are 16.50 ± 2.10 h and 8.20 ± 1.30 h, respectively.

The circadian activity pattern

Figure 2 shows an example of the activity pattern during one observation period of 24 h. The numbers sighted were registered every 15 min. The evident irregularities are quite typical of rabbit emergence in this site and consistent with our observations of individual rabbits re-entering and re-emerging from burrows during the night.

To determine the existence of short-term periodicities, sample autocorrelations (Chatfield 1975) were calculated for 3 series of observations over 24 h. Fig. 3 shows that the only significant correlations are between one observation and the subsequent one to five observations.

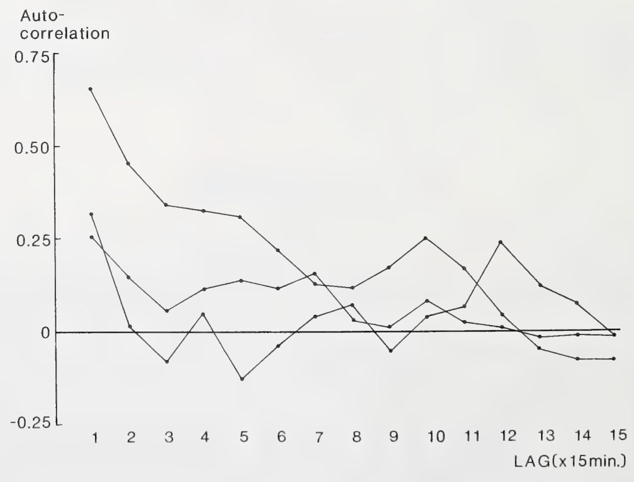


Fig. 3. Autocorrelation function for activity per 15 min on 3 dates (Oct. 1979, Oct. 1980, Dec. 1980). Only the period that the rabbits are active is used. n = 74. 90 % confidence limits = ± 0.23

Seasonal changes in the percentage of rabbits active

Figure 4 is constructed by averaging the monthly observations from the three years (only for those months for which assessments of population size were available). For each year the mean number of rabbits for the observation sessions (in each 2 hour period) is converted to a percentage of the population by dividing by the population size for that particular month. The percentages of rabbits active in corresponding time periods are then averaged for the three years. The figure illustrates the trend in activity over the year. Activity is low in wintertime and increases at the beginning of March.

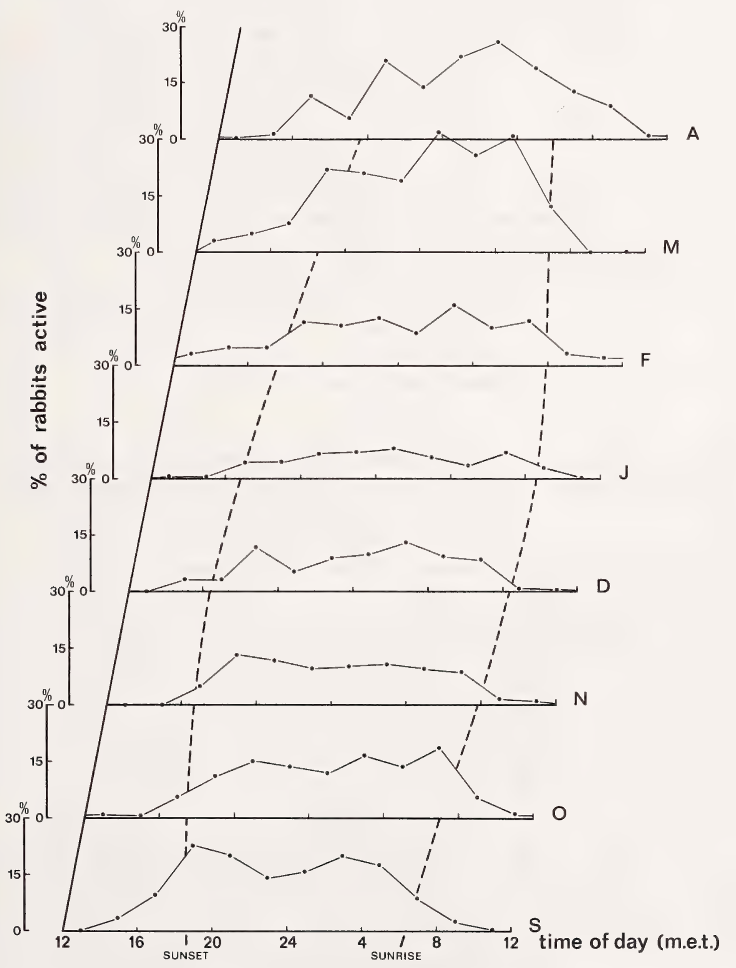


Fig. 4. Average activity patterns for each month between September and April. Each point is the mean of 3 observations made in different years

A homogeneous distribution of activity between 18.00–6.00 h can be confirmed or refuted by dividing this period into three equal parts (per day) and comparing the first and second part with Wilcoxon matched-pairs signed-ranks (Siegel 1956). This statistic does not require that the rabbits behave independently of each other. It is computed both for the whole series and for the separate seasons. In all cases $p > 0.05$, so there is no significant tendency to bimodality.

Table 1. **Average activity (hours above ground) per rabbit in 24 hours**

Full-grown rabbits only

year	1979	1980	1981	1982	average
January		–	0.9	1,4	1,2
February		3,1	1,3	1,2	1,9
March		2,9	4,5	2,6	3,3
April		3,3	2,9	2,4	2,9
May		4,8	–		4,8
June		5,0	–		5,0
July		–	–		
August	–	–	–		
September	–	3,2	2,3		2,8
October	2,9	1,9	1,9		2,2
November	1,6	1,5	2,1		1,7
December	–	1,8	0,5		1,2

Sept. + Oct. versus Nov. to Feb.: p = 0.02; March + April versus Nov. to Febr.: p = 0.02 (Mann-Whitney-U-test)

The average period spent above ground per individual is calculated for each month by summing the mean number of active rabbits per hour and dividing this total by the known population size for that month (Tab. 1). From November to February it is only 1.5 h, in March and April 3.1 h. It may be even higher during the summer months.

Maximum number of active rabbits

To calculate the theoretical results of the sight count method, I have taken the maximum value of 5 consecutive 15 min sightings starting or ending with at 1 h after sunset or 1 h before sunrise, respectively, and divided it by the population size and multiplied it by 100/70 to get the percentage of the population above ground (Table 2).

The data in Table 2 show that the rabbits were never all above ground at the same time. Generally, the percentages in January are lower than in either September or March.

Fluctuations are smaller just after sunset (from 5–57 %) than just before sunrise (from 0–77 %).

Table 2. **The percentage of the total population which is active, one hour after sunset and one hour before sunrise. The highest value of five consecutive observations is given**

Full-grown rabbits only

	Highest percentage of the population observed							
	at 1 hour after sunset				at 1 hour before sunrise			
year	1979	1980	1981	1982	1979	1980	1981	1982
January		5	8	24		5	8	24
February		20	27	34		31	45	34
March		48	48	24		34	76	–
April		48	55	27		16	77	27
May		57	–	–		48	–	–
June		44	–	–		–	–	
July		–	–			–	–	
August		–	–			–	–	
September	35	38	22		–	24	29	
October	40	35	16		33	22	29	
November	30	28	28		8	28	9	
December	–	34	11		–	27	0	

Discussion

Start of activity

Our results show that emergence time varies, but does not correlate with the time of sunset as would be expected from experiments and observations on synchronization of activity periods of wild rabbits with daily variations in colour and light intensity of the sky (Nuboer et al. 1983). This 'non-synchrony' was also found in summertime in the hare (Holley and Greenwood 1984).

This is partly due to the fact that in my study area foraging areas were adjacent to the burrows. NUBOER et al. (1983) recorded the movement from hutch to food supply (indoors) or between the warren in the dune and feeding site on the floodplain. I took emergence out of the burrow to be 'start of activity'. In my study site we saw rabbits re-enter or re-emerge from their burrows during the night. This has also been noted by MYKYTOWYCZ and ROWLEY (1958) and KRAFT (1978).

Another reason for the lack of synchrony may be the influence of weather. ROWLEY (1957) found a late emergence during strong winds and/or rain. KOLB (1986) mentions an extremely variable onset of activity for rabbits in a small enclosure. He found a negative correlation with the maximum temperature during the previous day.

In particular a change in the type of weather is expected to influence emergence time. An example is the influence of changes in cloud cover on suckling behaviour of hares (*Lepus europaeus,* Pallas) (BROEKHUIZEN and MAASKAMP 1980). The influence of the period of the moon has been analysed only by LORD (1964) on *Sylvilagus*. He did not find any effect on activity pattern.

I did not find a significant correlation between either emergence time or maximum percentage active with temperature, wind speed or length of showers. However, the data collected were not sufficient for a detailed analysis of the influence of weather conditions. During the fieldwork I did notice that directly after snowfall rabbits stayed underground at night and that during prolonged snow periods the entire population may be above ground in the afternoon.

The circadian activity pattern

The rabbits' eyesight is good at low light intensity. Their sensitivity to the "blue" and "green" parts of the spectrum and their "blue-green" dichromacy seems an adaptation to the light environment during twilight (NUBOER et al. 1983). One would expect the highest activity in twilight, and therefore a bimodal activity pattern.

HOF et al. (1963) did indeed find this pattern for locomotor activity in domestic rabbits. RIETVELD et al. (1964) showed that changing the irradiance abruptly gave more pronounced activity peaks. PRUD'HON and GOUSSOPOULOS (1976) measured locomotor and foraging activity in indoor cages and KRAFT (1978) 'total activity' and foraging activity in small outdoor enclosures. Both compared wild to domestic rabbits in this respect. Wild rabbits showed one phase of nearly uninterrupted activity, with more (KRAFT) or less (PRUD'HON and GOUSSOPOULOS) pronounced bimodal foraging peaks. Domestic rabbits changed phases of rest and activity a few times during 24 hours. BROEKMEYER and LUNEN (1986) saw that they kept this pattern after release in the wild. It is thus not advisable to study the behaviour of domestic rabbits to get more insight into that of their wild relatives.

When, in experiments under controlled light conditions, a bimodal pattern for either locomotor or foraging activity is not obvious, it does not surprise us that workers studying overall activity of (more or less) free-living rabbits report no peaks. Generally they find rabbits to be equally active the whole night (STODART and MYERS 1964; MYERS and POOLE 1961, this study). A similar unimodal activity period is also found in the related *Sylvilagus* (LORD 1964) and *Lepus timidus* (LEMNELL and LINDLÖF 1981).

Interpretation of sight counts

Data on activity levels can be useful to people monitoring rabbit populations by sight counts. Fig. 4 can be used to choose the best time for counting.

People wishing to count rabbits on their land often start at either 1 h after sunset or 1 h before sunrise. Table 2 gives the proportion of rabbits active at these times.

One will have to correct for the proportion of the terrain that is visible, especially when

comparing counts done in different areas. Here I will only consider the influence of the circadian and yearly activity patterns on the chance that a rabbit is above ground.

Different figures have been given for the maximum proportion above ground at any one time: Dunnet (1957) 55–60 %, Lésel (1968) 50 %, Myers (1957) 90 %, Mykytowycz and Rowley (1958) 66 %, Schantz and Liberg (1982) 57 %, Southern (1940) 'usually' 30 % and in this study 5–57 %.

Gibb et al. (1978) found a large effect due to population density: at a high density with food shortage 90–95 % were above ground, at a low density only 45 %. This is, however, different from the situation in our dunes, where a possible food shortage coincides with the coldest time of the year and being above ground costs energy.

The influence of the weather on short-term fluctuations in the maximum percentage active is probably not as strong as its influence on time of emergence. Gibb et al. (1978) found that only wind speeds higher than 6 Bf had an influence on numbers above ground.

For the same population as described here, Geut and Jansen (1980) made 4 series of at least 9 consecutive morning and evening observations. They found that highest daily maxima occurred where there was no or very little rain and low wind speed, and lowest maxima occurred after rainfall. Temperature and wind direction seemed to have no effect.

Seasonal changes in activity

The level of activity varies strongly with the seasons. Activity reachs a nadir in wintertime, followed by a strong increase in March. The increase corresponds with the onset of reproduction in the study area (Wallage-Drees 1983: 50 % of does pregnant in the first week of March, so 50 % lactating in the first week of April). Lactating requires a lot of energy (2 to 3 times the demands for maintenance, Reyne et al. 1977). Thus does need more food at that time and, consequently, will forage longer. Lloyd (1964) mentions a longer feeding period in pregnant does compared to other rabbits active at the same time.

The short activity period in winter is a surprise, the more so since domestic rabbits (3 kg) who had access to food for only 4 h a day, lost weight. The coldest night during this study was in December 1981. The temperature dropped from 0 to −8 °C. The associated activity pattern, with hardly a rabbit above ground after 23.00 h, was the most extreme. This means that foraging time was short where one would have expected rabbits to need more time to gather a sufficient quantity of good quality food (Wallage-Drees and Deinum 1986).

The demand for food in winter is determined by diametrically opposed factors. Rabbits do not have a large fat reserve (mean: 7–21 g, Wallage-Drees 1986). The energy requirement in winter is less than in other seasons because there is hardly any sexual, aggressive or burrowing behaviour. On the other hand energy is needed to keep the body temperature stable. In domestic rabbits basal metabolism increases 1,5 times when outdoor temperature drops from 14 °C to 4 °C (Kleiber 1975). Wild animals that have had time to adapt compensate partly by enhancing their fur thickness (insulation, Hart et al. 1965). Also keeping the fur dry, avoiding strong winds and staying in their burrows will help to reduce heat losses. The burrow presents an environment of moderate, stable temperatures (Hayward 1961). In this dilemma the Dutch rabbits choose to stay underground for many hours a day.

The rabbit originates from the Mediterranean. They have been extensively studied in Australia, where they are very successful in areas with climates resembling that of the Mediterranean (Myers 1971). Rabbits are also successful in coastal dunes. It looks as if they have adapted to our climate by showing low activity in winter and becoming diurnal on the coldest days.

Acknowledgements

Dr J. F. W. Nuboer (RUU) stimulated the observation of wild rabbits. The PWN, manager of the N-H D, assisted in many ways with the fieldwork. I thank dr S. Broekhuizen, drs. G. J. de Bruyn, dr N. Croin Michielsen, dr E. v. d. Meijden and prof. dr K. Bakker for their advice and interest during the study. H. Heijn made the graphs. And many helped in gathering the data, in good or bad weather and at the most impossible times of the day and night: Reinier Akkermans, René Bakker, Theo Bakker, Jan Damm, Wim Denneman, Dory van Dierendonk, Glenn Dinsbach, Frank Distelbrink, Corrie Elders, Dorien Farjon, Gerda Geut, Heleen Goddijn, Adriaan Guldemond, Cor ten Haaf, Herman Immink, Anthony James, Els Jans, Elsje Jansen, Marielle Jansen, Nico Jonker, Yvonne van Manen, Jan van Mourik, Jaap Mulder, Michiel van Nierop, Sari van Noorden, Jan Roggeveen, Marjon Rutz, Mies Schollaard, Maud Scholten, Margriet Stapel, Dirk Tanger, Henny van Veen, Sjaak de Waard, Anton Weeda, Hans van de Water, Willem de Wart.

Zusammenfassung

Eine Feldstudie über saisonale Änderungen der circadianen Aktivität von Kaninchen

Wilde Kaninchen sind in der Nacht aktiver als Hauskaninchen. Der Zeitpunkt ihres Erscheinens und Verschwindens ändert sich nicht mit Sonnenuntergang und Sonnenaufgang; er bleibt während des Jahres ungefähr gleich.

Definieren wir ‚aktiv' als die oberirdische Anwesenheit, dann haben wilde Kaninchen nur *eine* aktive Periode mit unregelmäßigen Schwankungen während der Nacht.

Vergleichen wir die durchschnittliche Zeit, die ein Kaninchen während des Jahres oberirdisch verbringt, dann zeigen sich große Unterschiede zwischen dem Zeitabschnitt November/Februar und den anderen Monaten. Die Ursachen dafür werden besprochen.

Das Maximum im Anteil aktiver Kaninchen während eines Tages ist im Winter niedriger als in den übrigen Monaten. Dem muß man Rechnung tragen, wenn man die Größe der Population abschätzt.

References

Broekhuizen, S.; Maaskamp, F. (1980): Behaviour of does and leverets of the European hare *(Lepus europaeus)* whilst nursing. J. Zool. (Lond.) **191**, 487–501.

Broekmeyer, M.; Lunen, K. van (1986): Een onderzoek naar het effect van konijnen op de vegetatie van de Derde Duintjes, Boschplaat, Terschelling. Hugo de Vrieslab., Univ. Amst., intern. rep. **206.**

Chatfield, C. (1975): The analysis of time series: theory and practice. London: Chapman and Hall.

Dunnet, G. M. (1957): Notes on emergence behaviour of the rabbit *Oryctolagus cuniculus* (L.) and its bearing on the validity of sight counts for population estimates. CSIRO Wildl. Res. **2**, 85–89.

Feen, P. J. van der (1963). Hoe en wanneer zijn wilde konijnen in Europa verspreid geraakt? Biologisch Jaarboek **31**, 237–243.

Geut, G.; Jansen, M. (1980): Enkele aspecten van de oecologie van het wilde konijn (*Oryctolagus cuniculus* (L.)). Intern. rep., Univ., Groningen.

Gibb, J. A.; Ward, D.; Ward, C. P. (1978): Natural control of a population of rabbits, *Oryctolagus cuniculus* (L.), for ten years in the Kourarau enclosure. Dept. Sci. Ind. Res., Bull. **223.**

Hart, J. S.; Pohl, H.; Tener, J. S. (1965): Seasonal acclimatization in Varying Hare *(Lepus americanus).* Can. J. Zool. **43**, 731–744.

Hayward, J. S. (1961): The ability of the wild rabbit to survive conditions of water restriction. CSIRO Wild. Res. **6**, 160–175.

Hof, M. W. van; Rietveld, W. J.; Tordoir, W. E. M. (1963): Influence of illumination on locomotor activity of rabbits. Acta Physiol. Pharmacol. Neerl. **12**, 266–274.

Holley, A. J. F.; Greenwood, P. J. (1984): The myth of the mad March hare. Nature, Lond. **309**, 549–550.

Hörnicke, H.; Dietzel, F.; Aigner, E.; Schulte, R. (1976): Alimentary behaviour in rabbits under different influences. 1er Congr. Int. cunicole, Dyon, commun. **13**,.

Kleiber, M. (1975): The fire of life. Huntington, New York: R. E. Krieger.

Kline, P. D. (1965): Factors influencing roadside counts of cottontails. J. Wildl. Manage. **29**, 65–671.

Kolb, H. H. (1986): Circadian activity in the wild Rabbit *(Oryctolagus cuniculus).* Mammal Rev. **16**, 145–151.

Kraft, R. (1978): Beobachtungen zur Tagesperiodik von Wild- und Hauskaninchen. Z. Säugetierkunde **43**, 155–166.

Lemnell, P. A.; Lindlöf, B. (1981): Diurnal and seasonal activity pattern in the mountain hare. Ed. by K. Myers and C. D. MacInnes. Proc. First World Lagomorph Conf., Guelph, Ontario. pp. 349–356.

LESEL, R. (1968): Essai d'estimation de la population d'*Oryctolagus cuniculus* L. sur la Peninsula Courbet (Iles Kerguelen). Mammalia **32**, 612–620.
LLOYD, H. G. (1964): Influences of environmental factors on some aspects of breeding in the wild rabbit, *Oryctolagus cuniculus* (L.). MSc thesis, University of Wales.
LOCKLEY, R. M. (1964): The private life of the rabbit. Worcester, London: Baylis and Son.
LORD, R. D. (1964): Seasonal changes in the activity of penned cottontail rabbits. Anim. Behav. **12,** 38–41.
MYERS, K. (1957): Some observations on the use of sight counts in estimating populations of the rabbits, *Oryctolagus cuniculus* (L.). CSIRO Wildl. Res. **2,** 170–171.
— (1971): The rabbit in Australia. In: Proc. adv. study inst. 'Dynamics of Numbers in Populations'. Oosterbeek, The Netherlands. Ed. by P. J. DEN BOER and G. R. GRADWELL. pp. 478–507.
MYERS, K.; POOLE, W. E. (1961): The effects of season and population increase on behaviour. CSIRO Wildl. Res. **4,** 14–26.
MYKYTOWYCZ, R.; ROWLEY, I. (1958): Continuous observations of the activity of the wild rabbit, *Oryctolagus cuniculus* (L.), during 24-hour periods. CSIRO Wildl. Res. **3,** 26–31.
NIETHAMMER, G. (1938). Ergebnisse von Markierungsversuchen an Wildkaninchen. Z. Morphol. Ökol. Tiere **33,** 297–312.
NUBOER, J. F. W. (1971): Visual acuity measurements in a rabbit. PhD thesis, Univ. Utrecht.
NUBOER, J. F. W.; NUYS, W. M. VAN; STEENBERGER, J. C. VAN (1983): Colour changes in a light regimen as synchronizers of circadian activity. J. comp. physiol. **151,** 359–366.
PRUD'HON, M.; GOUSSOPOULOS, J. (1976): Comportement alimentaire du lapin de garenne en captivité. Ann. Zootech. **25,** 407–410.
REYNE, Y.; PRUD'HON, M.; DEBICKI, A. M.; GOUSSOPOULOS, J. (1977): Caracteristiques des consommations d'aliments solide et liquide chez la Lapine gestante puis allaitante nourrie ad libitum. Ann. Zootech. **27,** 211–223.
RIETVELD, W. J.; TORDOIR, W. E. M.; HOF, M. W. VAN (1964): Influence of light to dark ratio, for a 24-hour cycle, on locomotor activity of rabbits. Acta Physiol. Pharmac. Neerl. **13,** 87–95.
ROWLEY, I. (1957): Observations on evening rabbit activity in relation to weather and sunset. CSIRO Wildl. Res. **2,** 168–169.
SANDERSON, J.; VANDERWEELE, D. (1975): Analysis of feeding patterns in normal and vagotomized rabbits. Physiol. Behav. **15,** 357–364.
SCHANTZ, T. VON; LIBERG, O. (1982): Censusing numbers of medium-sized nocturnal mammals in open landscapes. Proc. XIV Int. Wildl. Congr., Dublin, 1979. pp. 409–417.
SIEGEL, S. (1956): Nonparametric statistics for the behavioral sciences. Kogakusha: McGraw-Hill.
SNYDER, W. I. (1978): Feed constituent digestibility by adult and juvenile cottontail rabbits. PhD thesis, Department of Natural Resources, Univ. Cornell, Cornell.
SOUTHERN, H. N. (1940): The ecology and population dynamics of the wild rabbit *(Oryctolagus cuniculus).* Ann. appl. biol. **27,** 509–526.
STODART, E.; MYERS, K. (1964): A comparison of behavior, reproduction and mortality of wild and domestic rabbits in confined populations. CSIRO Wildl. Res. **9,** 144–159.
TITTENSOR, A. M.; WOODS, J. A.; FOX, A. P. (1978): Ecology of farmland rabbit populations. Pest Infestation Control Laboratory Report 1974–76, pp. 155–157. London: HMSO.
WALLAGE-DREES, J. M. (1983): Effects of food on onset of breeding in rabbits, *Oryctolagus cuniculus* (L.), in a sand dune habitat. Acta zool. Fenn. **174,** 57–59.
— (1986): Seasonal changes in the condition of rabbits, *Oryctolagus cuniculus* (L.), in a coastal sand dune habitat. Z. Säugetierkunde **51,** 26–36.
WALLAGE-DREES, J. M.; DEINUM, B. (1986): Quality of the diet selected by wild rabbits [*Oryctolagus cuniculus* (L.)] in autumn and winter. Neth. J. Zool. **36,** 438–448.
ZEUNER, F. E. (1963): A history of domesticated animals. London: Hutchinson. pp. 409–415.

Author's address: Drs J. MARIJKE WALLAGE-DREES, Department of Population Biology, University of Leiden, P. O. Box 9516, NL-2300 RA Leiden, The Netherlands

Z. Säugetierkunde 54 (1989) 31–39

ISSN 0044-3468

Feeding habits of the Water mongoose *(Atilax paludinosus)*

By Carolyn M. Baker

Biology Department, University of Natal, Durban

Receipt of Ms. 24. 8. 1987

Abstract

Water mongooses are solitary, nocturnal herpestines that are found mainly in close proximity to water. The diet of free-living mongooses was assessed through scat analysis. Results show crabs to be the most important component, followed by amphibians and small mammals. Food tests on captive *Atilax* indicated a preference for rodent and amphibian prey. Methods of prey capture are described and the efficiency with which a variety of prey types are handled is discussed. Factors allowing coexistence with other herpestines and also other carnivores are mentioned. It is suggested that the dietary flexibility of *Atilax* resembles that of the ancestral herpestines, and represents the dietary preadaptations that were required by sociable herpestines for their shift towards group life.

Introduction

Details concerning the diet of *Atilax paludinosus* are provided by Rowe-Rowe (1978), Du Toit (1980), Whitfield and Blaber (1980), Louw and Nel (1986) and MacDonald and Nel (1986). Feeding habits are mentioned only in general references (Smithers 1971; 1983; Ewer 1973; Rosevear 1974; Stuart 1981). In the present report details of diet of both captive and free-living mongooses, as well as food preferences and prey-catching behaviour of captive animals, are given. In addition an attempt is made to show the significance of the diet of this herpestine against the background of its solitary, nocturnal nature.

Material and methods

Eight mongooses were housed in enclosures measuring 1,5 × 3 × 1,2 m. Their origins and capture information are reported in Baker (1987) and Baker and Meester (1986). Animals were maintained on a diet of day-old chicks, rats and *Xenopus* (clawed toads). On occasion crabs (*Potamonautes* sp.), chicken's eggs, Orthoptera and oxheart were provided. Each enclosure was supplied with a galvanised iron bath which served as both a pond and a continuous water supply.

In food preference tests the mongooses were offered a choice of two freshly-killed prey items. Prey was killed using carbon dioxide rather than ether, to avoid selection owing to an unfamiliar odour. The items were killed to prevent a biased choice owing to differences in movement or sound patterns. Those used in the tests included insects, crustaceans, amphibians, birds, chicken's eggs and rodents. Each choice test was replicated five times. In each case the item that was taken first by the animal was presumed to represent the preferred food.

In order to observe prey-catching behaviour live prey was introduced into the mongoose enclosures. Time elapsed from detection of prey until attack, and from initiation of the attack until the prey was dispatched, was recorded.

Details of prey-catching behaviour varied slightly from one prey type to another. However, several elements were common to all sequences. Prey-catching was divided up into two components:

1. Sighting. This was inferred from the stance of the mongoose, which included erection of ear pinnae, tautening of the body and, on occasion, piloerection.
2. Attack. The attack commenced when the mongoose started to stalk or chase the prey, and terminated when the prey had been killed. Death was deduced from the prey's lack of movement. Several components of the attack were recognised, namely the stalk, the pounce and the kill.

For each prey type the behaviour patterns used to catch and kill the prey were noted.

Details of the diet of free-living water mongooses were obtained by scat analysis. Monthly samples of scats were collected from Kenneth Stainbank Nature Reserve in Durban from May 1984 until

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5401-0031 $ 02.50/0

Table 1. **Results of food preference tests**

Choice	Preference	Percentage
day-old chick	3	12
amphibian	22	88
	n = 25	
day-old chick	1	4
chicken's egg	24	96
	n = 25	
day-old chick	23	92
crab	2	8
	n = 25	
day-old chick	0	0
rodent	25	100
	n = 25	
amphibian	11	44
rodent	14	56
	n = 25	
chicken's egg	7	41
rodent	10	59
	n = 17	
crab	2	13
rodent	13	87
	n = 15	
amphibian	7	28
chicken's egg	18	72
	n = 25	
amphibian	11	79
crab	3	21
	n = 14	
insect	2	20
crab	8	80
	n = 10	
insect	0	0
amphibian	10	100
	n = 10	
insect	0	0
rodent	10	100
	n = 10	

February 1985. After collection the scats were frozen until they were prepared for analysis. Preparation included thawing, oven-drying at 50 °C for at least five days and then sorting by dissection microscope into taxonomic categories. Vertebrate prey was identified by the presence of hair (mammal), feathers (bird), scales (fish or reptile) or skeletal elements (amphibians). The distinction between different kinds of invertebrate prey (crab and insects) was easily made as crab exoskeleton is particularly distinctive. Within the Insecta identification to order was made whenever possible. Fruits were identified by their seed types. For the present study no attempt was made to determine proportions of the various food items and only relative percentage frequency of occurrence is reported. This statistic was calculated by totalling all occurrences (ie. presence or absence in each scat) and expressing actual occurrence of each item as a percentage of the total.

Results

Results of food preference tests are presented in Table 1, and of scat analysis in Table 2 and 3. Details regarding prey capture are presented in Table 4.

When crabs were introduced into the ponds, detection occurred only when the mongooses either swam in or walked past the water. Once the prey had been sighted the mongooses systematically began to "feel" over the base of the pond to locate the prey. Their heads were never immersed during this part of the search and only when the crab was located did they duck their heads under the water to catch the prey. Thus the feet were used in prey location and the mouth in grabbing. The orientation of the bite varied but as soon as the prey was firmly held it was removed from the water and dealt with on the ground. This involved pinning the crab down and biting it. Most commonly the claws were removed first, presumably to prevent injury to the mongoose. Occasionally the crab was tossed aside and then retrieved before being eaten. Rowe-Rowe (1978) suggests that this may serve to stun and temporarily disorient prey, thus facilitating killing. Occasionally also it was picked up between the forefeet and thrown on to the ground to facilitate its fragmentation and death. The entire crab was usually consumed, although in particularly large specimens parts of the carapace were often discarded.

Rodent prey was located by either sight or sound. An initial hesitation usually occurred after detection and was followed by a quick dash and pounce. The killing bite was administered to the head region and commonly spanned the antero-dorsal part of the cranium. "Repeat biting" was not commonly observed in adults although it was occasionally exhibited by juveniles. After the killing bite had been administered the prey was often

Table 2. **Occurrence of food items in 34 scats**

Food item	Occurrence	Relative % freq of occurrence
Crustacea	26	22
Insecta	25	21,1
Amphibia	22	18,6
Small mammal	12	10,1
Aves	11	9,3
Reptilia	4	3,3
Diplopoda	4	3,3
Pisces	2	1,6
Chilopoda	2	1,6
Fruit	2	1,6
Mollusca	1	0,8
Miscellaneous	7	5,9

Table 3. **Occurrence of various insects in 25 scats**

Insecta	Occurrence	Relative % frequency Occurrence
Insecta unidentified	5	10,6
Orthoptera	14	29,7
Coleoptera	17	36,1
Lepidoptera	6	12,7
Dermaptera	2	4,2
Isoptera	1	2,1
Odonata	1	2,1
Diptera	1	2,1

"shaken to death". It was usually consumed from the anterior end, although on occasion the tail was eaten or the throat opened first. In the case of large white rats the head was often mauled and then discarded. Some of the mongooses (one male and two females) often took their dead rodent prey into the ponds and played with them there (throwing them into the air, "drowning" them and nudging them) before consuming them out of the water.

Killing of amphibian prey varied depending on whether it was *Xenopus* or *Bufo* sp. *Xenopus* was located in the ponds by either sight or touch and treated in the same way as crab prey during the search. Only when the prey was located did the mongoose immerse its head in order to grab it. This prey is slippery and more elusive than crab prey and several misses usually occurred. When the amphibian was caught it was removed from the water, killed by a head bite and then kneaded on the ground. This behaviour was assumed to be aimed at removing the mucous body covering. In the case of *Bufo* sp. the prey was located by sight and killed by a head bite. Again these amphibians were palpated on the ground, presumably to remove any noxious substances. Occasionally "shaking to death" was recorded. When it had finished eating the mongoose cleaned its mouth by wiping it with the forefeet. This removed any mucous that had adhered to the vibrissae, lips and chin. *Bufo* sp. were not eaten as readily as *Xenopus* and in the field, in summer when *Bufo* congregate to mate, evidence was found of random killing. In one pond approximately ten dead frogs were found, each one decapitated and partially eaten. This was attributed to water mongoose as the sandy surrounds were covered with *Atilax* tracks.

Insect prey was usually located visually or aurally and was approached relatively casually. If the prey remained immobile the mongoose held it down with the forefeet and picked it up in the mouth. If the prey moved, however, the mongoose accelerated their attack. When within pouncing distance the prey was either caught in mid-air or pinned down by the forefeet and consumed immediately. Insect prey offered to the mongooses included orthopterans, isopterans, dictyopterans and coleopterans.

Table 4. **Sighting and attack times in prey-killing behaviour**

Prey item	Time taken to sight prey		Time taken to attack prey		Total attacks
	range	$\bar{x}$	range	$\bar{x}$	
Rodent	23–35s	21s	1–5s	3s	n = 5
Amphibia	25–279s	161,2s	45–56s	50,6s	n = 5
Crustacea	120–300s	204s	25–80s	49s	n = 5
Orthoptera	12–40s	23,4s	1–5s	3s	n = 5

The only live bird prey given to the mongooses were young chickens. These were located by sound, pursued and killed by a head bite. The entire prey was consumed. When dead adult pigeons were given to the mongooses the primary wing feathers and some tail feathers were usually discarded, as were the head and bill.

Chicken's eggs were broken by throwing them on the ground. This was accomplished by rearing up on the hind limbs and throwing the egg vertically downwards. In some cases when the eggs were particularly small the mongooses took the whole egg into the mouth and simply broke it open with the canines. The entire contents were eaten and in some cases even the shell was consumed.

Discussion

Scat analysis showed a preponderance of crab, insect and small mammal prey with amphibians and birds forming a significant part of the diet. While insects were frequently found in scats of free-living mongooses they formed a negligible portion of the bulk of the diet when compared with other food items. In food tests they were not a preferred food item. Two factors may account for this apparent lack of interest. Firstly, the prey given during food tests was dead and movement of insects seems to be an important stimulus for capture. Secondly, prey offerred at the same time as insects during food choice tests was always larger, energetically more rewarding, and thus more attractive to the mongooses. However, the tendency of small carnivores to exploit a variety of prey items should not be ignored, and in their natural habitat mongooses are likely to examine and consume any moving object provided that the effort expended in capture is not too great.

Food tests indicated a preference for rodent and amphibian prey. If only those tests in which naturally occurring items were considered (thus excluding choices containing chicken's eggs and day-old chicks) rodents were most frequently selected (44 % of the time) followed by amphibians (38 %), crabs (15.4 %) and finally insects (2.3 %). These results are particularly interesting when seen in the light of scat analysis results which reveal crabs to be the most abundant prey item. This suggests that while *Atilax* might prefer rodents, circumstances in the natural environment are not conducive to their exploitation. *Atilax* is a relatively large, solitary herpestine whose preferred habitat includes watercourses and nearby dense vegetation. The significance of this choice of habitat lies in the solitary nature of the mongooses and the associated need for cover from potential predators. For these reasons the most commonly encountered prey item is crabs, one which is furthermore under-utilized by any other co-existing species (MacDonald and Nel 1986). Further, the well-defined digits of *Atilax* are particularly well adapted to seeking out crabs that may be hidden beneath rocks and in crevices. Radinsky (1975) has shown that neocortical sulcal patterns in *Atilax* suggest increased tactile sensitivity and muscular control of the hands. It appears that these characteristics preadapt the water mongoose to its particular niche. In the field evidence of searching for prey in holes and crevices is exhibited by a concentration of tracks and footprints in the vicinity of crab holes in the mud along river banks.

The abundance of alternate food sources, such as amphibians and water-nesting birds, amongst the riverine vegetation provides an important secondary dietary component, and reduces the need to venture into the savannahs in search of prey. However, *Atilax* is not entirely restricted to stream areas. At Giant's Castle Nature Reserve (pers. obs.) and at Vernon Crookes Nature Reserve (Maddock, pers. comm.) *Atilax* moves from one stream bed to another across relatively open grassland. During these trips any terrestrial prey that is encountered may be taken, which may account for the relatively high occurrence of rodents in the scats, and illustrates the obvious preference for rodent prey. The only hazard in open country is lack of adequate cover for this large solitary herpestine.

Prey-catching tests reveal rodents to be the most rapidly noticed and dispatched food

items, while crabs offer more resistance during sighting and attack. While these results are consistent with the food preferences of *Atilax,* the abundance of crabs and the security offered by the sheltered environment within which crab-hunting occurs, must have survival implications for *Atilax* which are of greater consequence than the preference for rodents.

The strong preference for chicken's eggs in food tests may result from the apparent satisfaction that the mongooses derive from breaking them open. In a controlled captive environment with reduced stimulation, *Atilax* may approach egg-breaking more eagerly, simply as an activity to relieve boredom, rather than because eggs are a preferred food item. Evidence in support of this is shown by the frequent occurrence of stone throwing in captivity. Any small, hard object is investigated and thrown onto the ground. Because the behaviour persists beyond the time that would be required to open any food item, it is perceived (by the observer) as a "game" or as an energy releasing mechanism. While evidence for egg consumption from scat analysis is absent unless the shell is also consumed, bird's eggs may form an important part of the diet of free-living *Atilax,* albeit an irregular and unreliable one.

While *Atilax* relied on the interaction of several senses to capture prey, it appeared that sound and touch played the most important roles. Searching for aquatic prey was almost entirely a tactile exercise as visibility below water level was often reduced by turbulence, while detection of terrestrial prey was facilitated by audition. During live food tests the mongooses discerned the whereabouts of hidden terrestrial prey by standing still and listening for movement, evidenced by erect pinnae and slight alterations in head position. As soon as visual contact was made the attack commenced. Clearly sense of touch and hearing were detection mechanisms while vision played a follow-up role.

Variation in prey-catching methods is clearly related to the shape, activity and habitat of the different prey items. In the smaller herpestines (*Helogale undulata rufula:* Rasa 1973; *Galerella sanguinea:* Baker 1980) the killing bite for rodents is carefully directed at the eye and ear cavities. This is necessary for these small carnivores, as without a specifically oriented bite it would be difficult to penetrate the skull of the prey. In *Atilax,* however, the larger size of the jaws and teeth as well as the more powerful jaw action easily damages the skull, and so obviates the need for a well-oriented killing bite. This was evident also from the scats of free-living mongooses, in which complete or semi-complete skulls of vertebrate prey were never found.

Eisenberg and Leyhausen (1972) regard a precisely aimed killing bite as a recent advance in predatory behaviour whereas an undifferentiated bite with associated tossing or shaking is thought to be primitive. *Atilax* exhibits both an undifferentiated killing bite and "shaking to death", indicating that as far as prey-killing is concerned it should be considered a primitive herpestine. "Shaking to death" was not, however, an invariable behaviour pattern and was thought to be associated with the degree of hunger. When less hungry the mongooses were more inclined to play with their food, and in these circumstances "shaking to death" was frequently recorded.

"Food-washing" was often exhibited by several of the mongooses. Lyall-Watson (1963) discusses the function of this activity and suggests that it is a response to captivity. This behaviour was more common if the food given to the mongooses was not completely thawed, or if it was covered by sand and debris, thus suggesting a direct causal relationship between food condition and food manipulation.

The method of egg-breaking employed by *Atilax* is different from that of many other herpestines, which tend to throw the egg backwards between the hind limbs. Ewer (1973) discusses the evolution of these throwing patterns, and suggests that they have developed as a result of the animal's normal foraging patterns. Thus the "backward throwers" are usually those herpestines that scratch about for insects using a backward directed scratch, while the "vertical throwers" such as *Atilax* have dexterous "fingers" and are more likely to

succeed in holding the egg between the forefeet and to bite at it. In frustration they may rear up and drop the egg onto the ground, so initiating the tendency to throw downwards (Ewer 1973). Observations on young mongooses confirm this pattern; the earliest response to eggs was always an attempt at biting, and only later was the mature behaviour pattern learnt.

Sheppey and Bernard (1984) and Gittleman (1986) demonstrate that relative brain size appears to be related to feeding efficiency in carnivores. When comparing the

Table 5. **Percentage relative occurrence of food items in the diet of *Atilax***

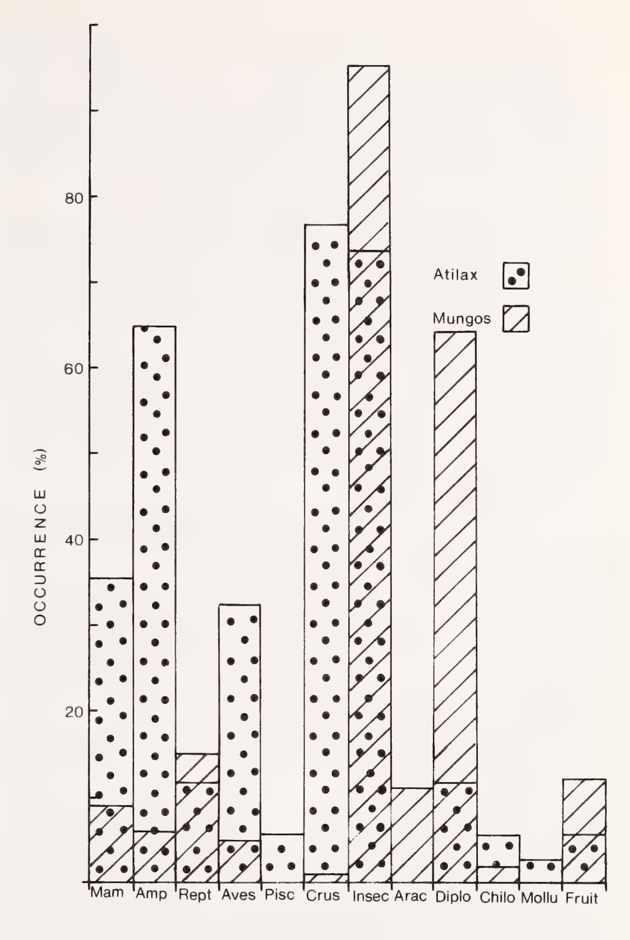
Food item	Whitfield and Blaber (1980)	Rowe-Rowe (1978)	Smithers (1983)	Baker present study	Louw and Nel (1986)			MacDonald and Nel (1986)
					Kobee Valley	Betty's Bay	Highland state For	
Crustacea	54,2	43	23,6	22	44,7	54,3	23,7	36,5
Amphibia	14,4	14	29	18,6	5,2	2,5	7,5	–
Mammalia	1,3	14	23,6	10,1	5,2	1,7	10	8,9
Aves	–	14	–	9,3	1,3	1,5	6,2	19,5
Reptilia	–	1	–	3,3	–	–	–	–
Pisces	7,2	2	4,5	1,6	26,3	2	5	10,6
Insecta	16,2	2	19	21,1	14,4	12,6	17,5	7,6
Mollusca	–	–	–	0,8	–	10,7	–	2,9
Myriapoda	–	–	–	5	–	–	–	1,7
Vertebrata unidentified	–	–	–	–	–	–	–	8,9
Plant	3,1	2	–	1,6	2,6	11,5	20	–
Carrion	–	5	–	–	–	–	–	–
Unidentified	3,1	3	–	5,9	–	2,5	10	2,9

Table 6. **Food items of major importance in the diet of various herpestines**

Herpestine	Activity period	Social structure	Food item	Habitat	Source
Ichneumia albicauda	N	Sol.	Insects	Savannah	Taylor (1972)
Herpestes ichneumon	D	Sol./ Co-op	Rodents	Wide tol./ Dense veg.	Stuart (1983) Delibes et al. (1984)
Atilax paludinosus	N	Sol.	Crabs	Dense veg.	Present study
Galerella sanguinea	D	Sol.	Insects	Savannah	Baker (1980)
Galerella bulverulenta	D	Sol.	Insects	Dense veg./ Savannah	MacDonald and Nel (1986)
Cynictis penicillata	D	Co-op.	Insects	Savannah	MacDonald and Nel (1986)
Mungos mungo	D	Soc.	Insects	Wide tol.	Sadie (1983)
Suricata suricatta	D	Soc.	Insects	Open/arid	Roberts (1981)
Helogale undulata	D	Soc.	Insects	Savannah	Rasa (1977) Smithers (1983)

N – Nocturnal; D – Diurnal

encephalization quotients of the herpestines it is clear that *Atilax* has the highest relative brain size, providing morphological evidence of its greater feeding efficiency. This is manifested in the variety of prey taken (Table 5) and the flexibility of prey-catching methods. This appears to be characteristic of all herpestines and demonstrates the adaptability that is common amongst small carnivores. However when comparing the food items of major importance in the diets of a sociable herpestine *(Mungos)* and *Atilax* (Fig.) it becomes clear that *Mungos* relies most heavily on grouped prey items, such as insects (Table 6). Solitary animals on the other hand are able to exploit a wider spectrum of prey of both small and large size, because the disturbance of prey caused by a group of foraging animals is not a factor that affects prey selection in solitary animals. Of significance in the diet of *Atilax* however, are the larger and more energetically rich prey items.



Percentage frequency of occurrence of food items in *Atilax* and *Mungos* scats. Data for *Mungos* taken from Sadie (1983). The % occurrence of insect prey for *Mungos* is underestimated due to the fact that Sadie did not record total occurrence, but noted the variety of prey taken

Various feeding strategies are available to large solitary herpestines, and strict reliance on large prey items is not the rule. *Ichneumia albicauda* is an herpestine of comparable size to *Atilax* and is also nocturnal. However this solitary animal is unusual in that it relies most heavily on insect prey and moves about mainly in savannahs (Smithers 1983). Over large areas within their range *Atilax* and *Ichneumia* co-exist (Rowe-Rowe 1978, Smithers 1983), but occupy mainly different habitats, *Ichneumia* occurring in savannah and *Atilax* along watercourses. Thus spatial separation and the associated exploitation of largely different food items are the two most important factors that allow coexistence of these two animals.

Another similar-sized coexisting and solitary herpestine is *Herpestes ichneumon*, whose diet tends towards small mammals (Stuart 1983; Delibes et al. 1984). Whether *H. ichneumon* is strictly solitary or whether it lives in small family parties is uncertain (Smithers 1983; Ben-Yaccov et al. 1986). Whatever the circumstances, diurnal activity is unusual for a large mongoose and protection from predators may be afforded by its

preferred habitat of dense vegetation close to water (Smithers 1983). It is, however, not uncommon in open grassland (Maddock, pers. comm.) which may account for its tendency towards group-living, in that predation risks would be reduced through increased alertness. Nevertheless, co-existence with *Atilax* and *Ichneumia* appears to be possible primarily as a result of temporal spatiation, and in addition because a preference for rodent prey precludes any competition.

These three examples illustrate a few of the patterns that result when activity regimen, habitat and diet are varied, and show that flexibility is characteristic of herpestines.

The ability of *Atilax* to exploit a variety of food items allows it to coexist compatibly not only with other herpestines (MacDonald and Nel 1986) but also with other carnivores that may be more specialised predators, for example *Aonyx capensis* and *Lutra maculicollis* (Rowe-Rowe 1978; van der Zee 1981). Louw and Nel (1986) report that virtually no overlap occurred in the diet of *Atilax* and *Aonyx* at Betty's Bay, with *Aonyx* taking prey of mainly marine origin, while *Atilax* utilized shore crabs and other terrestrial species. At St Lucia Whitfield and Blaber (1980) have shown that *Atilax* consume penaeid prawns, providing further evidence of dietary flexibility and the resultant occupation of divergent habitats.

Clearly, feeding patterns in *Atilax* are a consequence of several factors, the most important being its solitary mode of life, with habitat selection and availability of prey types being consequent upon this factor. When compared with other herpestines it is obvious that solitary representatives exploit a wider variety of food types (Table 6). If we follow current trends (Gorman 1979; Rasa 1986) and assume that group-living in herpestines is a recent development that was stimulated primarily as an anti-predator response when a shift into open country occurred, then the dietary flexibility of the ancestral, solitary herpestines, of which *Atilax* is a modern representative, preadapted those sociable species for group life, and their consequent shift in feeding patterns.

Acknowledgements

Thanks are due to Professor J. Meester for supervising the project and reading the manuscript; to Professor G. L. Maclean for translating the summary; Anthony Maddock for critical comments and useful discussions; Eleanor Richardson for caring for the animals in my absences; Ken Johnson for providing the crabs and frogs used in food tests; the South African Council for Scientific and Industrial Research and the University of Natal Research Fund for financing the project.

Zusammenfassung

Ernährungsgewohnheiten der Wassermanguste (Atilax paludinosus)

Wassermangusten sind einzellebende, nachtaktive Schleichkatzen, die meist am Wasser vorkommen. Die Zusammensetzung ihrer Nahrung im Freiland wurde durch Kotanalysen ermittelt. Die häufigsten Beutetiere waren Krabben, gefolgt von Amphibien und kleinen Säugetieren. Zweifachwahlversuche mit Beutetieren bei Wassermangusten in Gefangenschaft ergaben eine Bevorzugung von Nagetieren und Amphibien. Die Methoden des Beutefangs werden beschrieben, und die Fähigkeit, unterschiedliche Beutetierarten zu erlangen, wird erörtert. Umstände, die das Zusammenleben mit anderen Herpestinen erleichtern, werden erwähnt. Die Vielseitigkeit im Beuteerwerb bei *Atilax* dürfte dem ursprünglichen Zustand bei den Schleichkatzen nahekommen. Sie kann als Präadaptation an die Ausbildung eines differenzierten Gruppenlebens bei Herpestinen angesehen werden.

References

Baker, C. M. (1980): Biology and behaviour of the slender mongoose, *Herpestes sanguineus* (Rüppell, 1836). MSc. Thesis, Pietermaritzburg: Univ. Natal.

— (1987): The biology of the water mongoose *Atilax paludinosus*. PhD. Thesis (in prep.)

Baker, C. M.; Meester, J. (1986): Postnatal physical development of the water mongoose *(Atilax paludinosus)*. Z. Säugetierkunde **51**, 236–243.

Ben-Yaacov, R.; Yom-Tov, Y. (1983): On the biology of the Egyptian mongoose, *Herpestes ichneumon*, in Israel. Z. Säugetierkunde **48**, 34–45.
Delibes, M.; Aymerich, M.; Cuesta, L. (1984): Feeding habits of the Egyptian mongoose or Ichneumon in Spain. Acta Theriol. **29**, 205–218
Du Toit, C. F. (1980): The yellow mongoose *Cynictis penicillata* and other small carnivores in the Mountain Zebra National Park. Koedoe **23**, 179–184.
Eisenberg, J. F.; Leyhausen, P. (1972): The phylogenesis of predatory behaviour in mammals. Z. Tierpsychol. **30**, 59–93.
Ewer, R. F. (1973): The carnivores. London: Weidenfeld and Nicolson.
Gittleman, J. L. (1986): Carnivore brain size, behavioural ecology and phylogeny. J. Mammalogy **67**, 23–36.
Gorman, M. L. (1979): Dispersion and foraging of the small Indian mongoose, *Herpestes auropunctatus* (Carnivora: Viverridae) relative to the evolution of social viverrids. J. Zool. **187**, 65–73.
Louw, C. J.; Nel, J. A. J. (1986): Diets of coastal and inland-dwelling water mongoose. S. Afr. J. Wildl. Res. **16**, 153–156.
Lyall-Watson, M. (1963): A critical re-examination of food "washing" behaviour in the raccoon (*Procyon lotor* Linn.). Proc. Zool. Soc. Lond. **141**, 371–393.
MacDonald, J. T.; Nel, J. A. J. (1986): Comparative diets of sympatric small carnivores. S. Afr. J. Wildl. Res. **16**, 115–121.
Radinsky, L. (1975): Viverrid neuroanatomy: Phylogenetic and behavioural implications. J. Mammalogy **56**, 130–150.
Rasa, O. A. E. (1973): Prey capture, feeding techniques and their ontogeny in the African dwarf mongoose, *Helogale undulata rufula*. Z. Tierpsychol. **32**, 449–488.
— (1977): The ethology and sociology of the dwarf mongoose *(Helogale undulata rufula)*. Z. Tierpsychol. **43**, 337–406.
— (1986): Coordinated vigilance in dwarf mongoose family groups: The "Watchman's Song" hypothesis and the costs of guarding. Ethology **71**, 340–344.
Roberts, K. S. (1981): The foraging behaviour and strategies of the suricate *Suricata suricatta* (Erxleben). MSc. Thesis, Pretoria: Univ. Pretoria.
Rosevear, D. (1974): The carnivores of West Africa. London: Trustees of the British Museum, Natural History.
Rowe-Rowe, D. T. (1978): The small carnivores of Natal. Lammergeyer **25**, 1–48.
Sadie, D. (1983): The foraging behaviour and metabolic rate of the banded mongoose *Mungos mungo* (Gmelin). MSc. Thesis, Pretoria: Univ. Pretoria.
Shepherd, A. J.; Lemon, P. A.; Hartwig, E. (1983): Analysis of viverrid scats from the Northern Orange Free State. S. Afr. J. Zool. **18**, 400–401.
Sheppey, K.; Bernard, R. T. F. (1984): Relative brain size in the mammalian carnivores of the Cape Province of South Africa. S. Afr. J. Zool. **19**, 305–308.
Smithers, R. H. N. (1971): The mammals of Botswana. Museum Memoir No. 4. Salisbury: Trustees of National Museums of Rhodesia.
Smithers, R. H. N. (1983): The mammals of the Southern African subregion. Pretoria: Univ. Pretoria.
Stuart, C. T. (1981): Notes on the mammalian carnivores of the Cape Province, South Africa. Bontebok **1**, 1–58.
— (1983): Food of the large grey mongoose *Herpestes ichneumon* in the south-west Cape Province. S. Afr. J. Zool. **18**, 401–403.
Taylor, M. E. (1972): *Ichneumia albicauda*. Mammalian Species 12, 1–4. American Soc. Mammalogists 1972.
Whitfield, A. K.; Blaber, S. J. M. (1980): The diet of *Atilax paludinosus* (water mongoose) at St Lucia, South Africa. Mammalia **44**, 315–318.
Zee, D. van der (1981): Prey of the Cape clawless otter *(Aonyx capensis)* in the Tsitsikama Coastal National Park, South Africa. J. Zool. **194**, 467–483.

Author's address: Carolyn M. Baker, Zoology Department, Unsiversity of Durban-Westville, PB X 54001, Durban 4000, R.S.A.

Z. Säugetierkunde 54 (1989) 40–56

ISSN 0044-3468

The systematics of some Italian populations of Wild boar (*Sus scrofa* L.): A craniometric and electrophoretic analysis

By E. Randi, M. Apollonio and S. Toso

Istituto Nazionale di Biologia della Selvaggina, Bologna, Italy

Receipt of Ms. 3. 8. 1987

Abstract

Studied craniometric and electrophoretic characters of Italian and South-Western French wild boar (*Sus scrofa* L.) populations, compared with two samples of domestic pig, to assess their taxonomic relationships and to check the actual validity of the two Italian subspecies *S. s. majori* De Beaux and Festa, 1927, and *S. s. meridionalis* Major, 1883.

Nine craniometric traits from 41 skulls (from the ancient maremma, present Maremma and Sardinia populations) were submitted to univariate and multivariate statistic analyses. 200 wild boar specimens (from the Maremma, Sardinia and South-Western France populations) and 68 pig specimens (Landrace and Sardinian native free ranging breeds) were submitted to electrophoretic analysis.

Statistic analysis of such data has shown the Sardinian wild boar well separated from the overlapping clusters of the Italian populations. Multivariate analyses of the adjusted, Log- and Ratio-transformed data show a general overlapping of these groups. The main morphometric differences among the Italian, as well as the Western Palearctic wild boar populations, may be explained by a body size factor, probably linked to an environmental cline.

Electrophoresis has proven genetic characteristics of the studied wild boar samples at the loci LAP-Rbc and 6PGD. A dendrogram computed from the Nei's Ds shows a cluster, inclusive of the Italian Maremma and the French populations, well set apart from a second cluster with the closely linked Sardinian wild boar and Sardinian free ranging pigs. The Landrace breed and a wild population recently crossed with domestic pigs, appears very well separated.

As the Italian Maremma populations seem to belong to the same environmental cline of the Western Palearctic *Sus scrofa* populations, the opportunity to suppress the subspecies *S. s. majori* is suggested. The Sardinian wild boar is fairly well characterized morphometrically as well as genetically, so that the subspecies *S. s. meridionalis* must be maintained.

Introduction

In a monograph published in 1927, De Beaux and Festa described the new subspecies *Sus scrofa majori* dedicated to F. Major, the first who recognized its characteristics (Major 1885), to group apart the wild boar population living in the Tuscany and Latium Maremma (Italy). This population appeared to have a mean body size smaller than the nominate form *Sus scrofa scrofa* L. (Western Europe). In the same monograph the validity of the subspecies *Sus scrofa meridionalis,* proposed by *Major* in 1883, was used to describe the Sardinian wild boar population. This population, showing small body size, adapted to the poor environmental conditions of the island, posed continuous problems of identification and nomenclature (Strobel 1882; Major 1885; Miller 1912; De Beaux and Festa 1927), perhaps related to its possible origins from a breed of domestic pigs that became ferals and to the continuous interbreeding with the native free ranging domestic pigs (For a review see Apollonio et al., in press).

An immigration of wild boars from France (South-East) towards the Italian regions Liguria and Piedmont started in 1919. De Beaux and Festa (1927) pointed out these animals to belong to the nominate form *Sus scrofa scrofa* L. The distribution of wild boars in Italy around 1950 is shown in Fig. 1A. The peninsular populations filled a small portion of the potential area and were subdivided in well separated patches.

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5401-0040 $ 02.50/0

Following the decline they suffered from the XVII century to the early 1900's as a consequence of the extensive environmental modifications and of the hunting pressure man exerted, a cycle of quick expansion of the Italian wild boar populations then began.

The expansion was mainly due to the restocking for hunting purposes with animals from abroad (therefore belonging to different populations and probably to different subspecies as well). An almost continuous distribution from North-West (Piedmont) to South-West (Calabria) was achieved (Fig. 1B). The rearing of native domestic pig breeds in semi-wild conditions, as well as the purposive crossing between wild and domestic pigs, are considered to allow the diffusion of hybrid genotypes in the wild populations.

The methodological limitations of the works of MAJOR (1883, 1885) and DE BEAUX and FESTA (1927) as well as the demographic events the peninsular populations underwent, strongly suggest the opportunity to reconsider the systematics of the Italian wild boars.

Studying skulls from some German populations, attributed to the nominate form *Sus scrofa scrofa,* in comparison with samples from Italian and from Sardinian populations, the hypothesis of the existence of a dimensional cline linking the Western Palearctic populations, was raised (APOLLONIO et al., in press). The largest sizes are shown by the populations living around the North-Eastern end of the cline (Germany); the smallest sizes are shown by the populations living at the South-Western end of the cline (Central Italy and Sardinia Island, South France, South Spain). Such a dimensional trend (following the Bergman rule) may possibly by related to the diversity expressed by climatic and environmental conditions ranging from the Northern temperate decidous forest to the Southern semiarid Mediterranean scrub.

In this paper we have analyzed through univariate and multivariate statistics a sample of skulls from the Sardinian and from the Italian continental wild boar populations including some skulls (preserved in Museums) which had been partly studied by DE BEAUX and FESTA themselves. Our aim was to check if the Sardinian population could be morphometrically set apart from the peninsular ones and if the present Maremma populations retain the characteristics they showed when were a recognized as a new subspecies.

Moreover the genetic structure of several populations whose history is well known (from continental Italy, Sardinia and South-West France) was investigated through electrophoresis of blood and tissue proteins and enzymes. These samples were compared to those from domestic pigs belonging to an improved breed (Landrace) and to a sample from native Sardinian free ranging pigs.

The hypothesis of an environmental based dimensional cline of the Western Palearctic *Sus scrofa* populations was then contrasted with the electrophoretic data, in order to detect a possible genetic cline.

Material and methods

Blood and tissue samples were taken from captured, hunted or slaughtered animals belonging to the following populations (Fig. 1C).

1. San Rossore preserve (Pisa, Tuscany) = CSR (n = 109).
   The population of this preserve was originated in 1813 from a few animals belonging to the "Maremma" stock. In 1848 the population was decimated and afterwards, to aid a fast recovery, some free ranging pigs were introduced with a consequent crossing. A new population crash occurred in 1900 followed by a recovery. From that time until now only few animals have been introduced (1967) from the Castelporziano preserve. (n = sample size).
2. Castelporziano preserve (Rome) = CCP (n = 35).
   We have no information on introductions in this area. Probably this is the only true local nucleous and, because of its former geographic range, this population could be regarded as a relict of the *majori* subspecies.
3. Nuoro district (North-East Sardinia) = CSA (n = 9).
   In this range no introduction has occurred in the past with the exception of a few animals from Corsica in the 70's. However the Corsica and the Sardinia wild boars were formerly attributed to the same subspecies *meridionalis.*

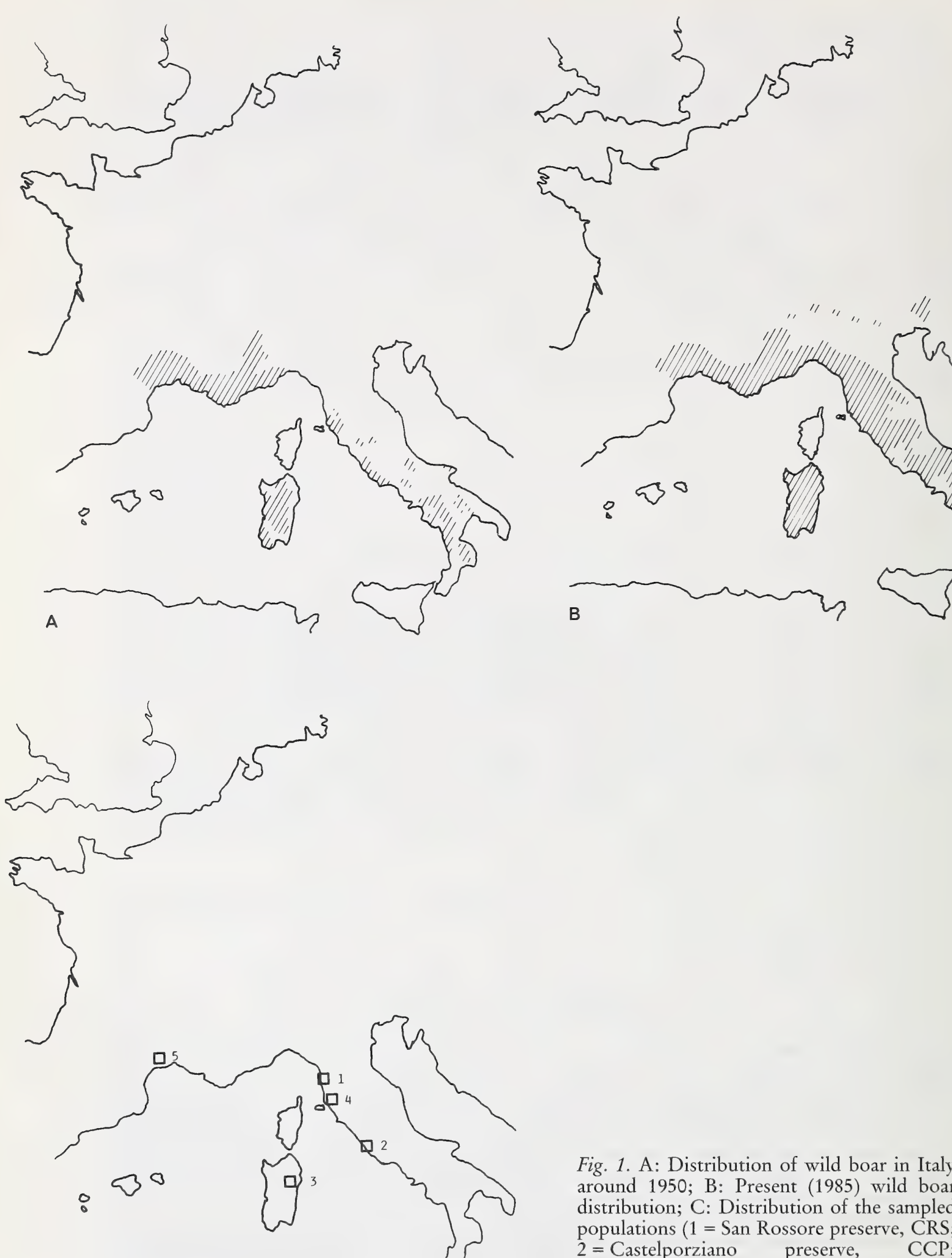


Fig. 1. A: Distribution of wild boar in Italy around 1950; B: Present (1985) wild boar distribution; C: Distribution of the sampled populations (1 = San Rossore preserve, CRS; 2 = Castelporziano preserve, CCP; 3 = Nuoro district, CSA; 4 = Natural Park of Maremma, CPM; 5 = South-West France, CFR)

4. Natural Park of Maremma (Grosseto, Tuscany) = CPM (n = 32).
   Until 1975 this area was a private hunting preserve. As before the World War II the local wild boars population was decimated by hunting and poaching, the owners planned to restock it with farmed wild boars crossed with domestic pigs (Boschi 1984). The present population shows phenotypic heterogeneity as a consequence of the past hybridization and a plan of selective cull is now carried out by the Park wardens.
5. France (South-West) = CFR (n = 15).
   Blood samples from hunted animals were obtained through the kind collaboration of Dr. G. Valet and Dr. F. Spitz (INRA, Laboratoire de la Faune Sauvage, Castanet Tolosan). They belong to populations living in several places of the Herault and Aude regions.
6. Landrace breed = MBO (n = 47).
   This sample of domestic pig was obtained from a local abbatoir (Bologna).
7. Sardinia native breed = MSA (n = 21).
   This is a sample of domestic pigs belonging to the native and free ranging Sardinian population.

Nine craniometric measurements (Tab. 1) were made on a total of 41 skulls of Italian wild boars partly belonging to the Sardinian population (CSA, n = 14♂♂; 3♀♀) and partly to the peninsular Maremma population. This sample consists of three groups:

1. Skulls (n = 13 ♂♂) belonging to the original Maremma population (CMAJ) studied by De Beaux and Festa (1927) for the identification of the subspecies *S. s. majori.* These skulls were obtained from the Natural History Museums in Milan, Florence, Turin, Genua and the Museum of the National Institute of Wildlife Biology and they include some of the specimens measured by Major (1885) and De Beaux and Festa (1927). They are therefore a sample of the Maremma population before any restocking was made.
2. Skulls (n = 8 ♂♂; 6 ♀♀) belonging to the San Rossore (CSR) preserve population, collected from hunted animals.
3. Skulls (n = 6 ♂♂; 8 ♀♀) belonging to the Castelporziano (CCP) preserve population, collected from hunted animals.

All skulls are from animals more than three years old as judged through the third molar tooth complete eruption and partial abrasion. Males and females were analyzed separately.

Size heterogeneity among the four groups was tested by analysis of variance of the observed means. An analysis of covariance (i. e. an analysis of variance applied to a linear regression model), was computed to check the presumed relationships between the length of the skull (expressed through its median superior length; character n. 3 in Tab. 1), and all the remaining craniometric variables. A set of regression coefficients, averaged over all the groups, is computed and used to adjust the group's means and the individual scores. A Snedecor's "F" test among the adjusted means was computed (Snedecor and Cockran 1967). The adjusted scores were used as input for multivariate analysis.

Multivariate relationships among groups were evaluated using two models (Morrison 1967). Principal Component Analysis (PCA) allows the description of the multivariate spatial distribution of the observed values within a cartesian system of vectors (PC) oriented along the successive maximum variability directions. The samples were analyzed as a single group in order to discriminate among group a-posteriori. The plot of the eigenvectors (loadings of the single variables) is a representation of the association pattern of the craniometric variables.

Canonical Analysis (CA) allows the visualization of the discrimination among a-priori determined groups, maximizing the between-groups versus the within-group variance. Within an orthogonal system of canonical variates (CV), the distances among groups are shown by the respective multivariate means (centroids) or by the distribution of the individual scores around their centroids.

Table 1. **List of the skull characters and acronyms of the studied samples**

1	= Condylobasal length.
2	= Overall length projected on the basal plane.
3	= Median superior length.
4	= Supraorbital width.
5	= Interorbital distance
6	= Width of nasal bones at maxillary-premaxillary suture.
7	= Height of skull with jaws clenched.
8	= Width of mandibula between condylear processes.
9	= Length of chin suture.
CSR	= San Rossore preserve, Pisa, Tuscany, (n. 1 in Fig. 1c).
CCP	= Castelporziano preserve, Roma, Latium, (n. 2).
CSA	= Nuoro district, Sardinia, (n. 3).
CPM	= Natural Park of Maremma, Grosseto, Tuscany, (n. 4).
CFR	= South-West France (n. 5).
MBO	= Domestic pig sample, Landrace breed.
MSA	= Sardinia native domestic pig breed.
CMAJ	= Sample of skulls belonging to the ancient Maremma population.

Multivariate analysis of the observed values was contrasted with multivariate analysis of the following data transformations:

1. Base-10 logarithms (Log), to correct for unequal character variances among groups linked to different sample size;
2. Ratios between each variable and the presumed general skull size (median superior length), to remove the influence of size variation among groups from the observed values;
3. Adjusted scores computed from the analysis of covariance, to remove the influence of size from the observed values.

Plasma, red blood cells (Rbc) and tissue homogenates (liver, heart) were submitted to electrophoresis following three techniques:

1. Polyacrylamide gel in horizontal slabs (PAGE) using an LKB (Bromma, Sweden) equipment;
2. Cellulose acetate membranes (CAM) using a Sartorius (Göttingen, W. Germany) equipment;
3. Vertical polyacrylamide gel in a discontinuous system (Davis 1964).

Buffer solutions and staining followed standard recipes (Tab. 2). A total of 33 loci were usefully resolved.

From the gels the allele frequencies were computed. Expected single locus heterozygosities, based on Hardy-Weinberg equilibrium, were tested against the observed heterozygosities (H_L), using a X^2 test. The mean heterozygosity over all the scored loci (H) was computed for each population, as well as the percent of polymorphic loci (P). A matrix of genetic distances among groups was computed

Table 2. **List of the studied loci and electrophoretic methods**

Locus[a]	Alleles[b]	Electro-phoresis[c]	Buffer	pH electro-de buffer	Method[d]	Tissues
1. G6PD	a	CAM	Tris-borate-EDTA	pH 8.7	A	Liver
2. LDH-A	a	PAGE	Tris-maleate	pH 7.4	B	Liver/Rbc
3. LDH-B	a	PAGE	Tris-maleate	pH 7.4	B	Liver/Rbc
4. AK	a	CAM	Phosphate	pH 6.25	A	Liver
5. GOT-S	a	PAGE	Tris-citrate II	pH 8.0	C	Liver
6. GOT-M	a	PAGE	Tris-citrate II	pH 8.0	C	Liver
7. MDH-S	a	PAGE	Tris-citrate II	pH 8.0	C	Liver/Heart
8. MDH-M	a	PAGE	Tris-citrate II	pH 8.0	C	Liver/Heart
9. ME-M	a	PAGE	Tris-citrate II	pH 8.0	C	Liver/Heart
10. ME-S	a	PAGE	Tris-citrate II	pH 8.0	C	Liver/Heart
11. SOD	a	PAGE	Phosphate-citrate	pH 5.9	B	Liver
12. PGM-1	a	CAM	Tris-maleate	pH 7.4	A	Liver/Rbc
13. EST-Rbc	a	PAGE	LiOH	pH 8.6	D	Rbc
14. IDH-S	a	PAGE	Phosphate-citrate	pH 5.9	B	Liver
15. IDH-M	a	PAGE	Phosphate-citrate	pH 5.9	B	Liver
16. ACP-1	a	PAGE	Tris-citrate	pH 8.0	B	Liver
17. ACP-2	a	PAGE	Tris-citrate	pH 8.0	B	Liver
18. α GPDH	a	CAM	Tris-borate-EDTA	pH 8.7	A	Liver
19. LAP-plasma	a	PAGE	LiOH	pH 8.6	D	Plasma
20. Pt-plasma 1	a	VERT	Disc. Davis	pH 8.3	E	Plasma
21. Pt-plasma 2	a	VERT	Disc. Davis	pH 8.3	E	Plasma
22. Pt-plasma 3	a	VERT	Disc. Davis	pH 8.3	E	Plasma
23. Pt-Rbc 1	a	VERT	Disc. Davis	pH 8.3	E	Rbc
24. Pt-Rbc 2	a	VERT	Disc. Davis	pH 8.3	E	Rbc
25. Pt-Rbc 9	a	VERT	Disc. Davis	pH 8.3	E	Rbc
26. Alb	a	VERT	Disc. Davis	pH 8.3	E	Plasma
27. Hb-A	a	VERT	Disc. Davis	pH 8.3	E	Rbc
28. Hb-B	a	VERT	Disc. Davis	pH 8.3	E	Rbc
29. PGI	a, b	CAM	Tris-borate-EDTA	pH 8.7	A	Liver
30. PGM-2	a, b	CAM	Tris-maleate	pH 7.4	A	Liver
31. 6PGD	a, b	PAGE	Phosphate	pH 7.0	B	Liver/Rbc
32. LAP-Rbc	a, b	PAGE	LiOH	pH 8.6	D	Rbc
33. Tf	a, b	VERT	Disc. Davis	pH 8.3	E	Plasma

[a] Loci nomenclature follows Harris and Hopkinson (1976). – [b] a = fast allele, b = slow allele. – [c] PAGE = polyacrylamide gel electrophoresis; CAM = cellulose acetate membrane electrophoresis; VERT = vertical polyacrylamide gel electrophoresis. – [d] A = Grunbaum (1981); B = Harris and Hopkinson (1976); C = Selander (1971); D = Ferguson (1980); E = Davis (1964)

Table 3. **Mean values and adjusted means of the studied skull characters (males only)**

Character[a]	CSA (n = 14)[b]		CMAJ (n = 13)		CSR (n = 8)		CCP (n = 6)		"F"-test	
	Obs[c] (± 1 s.e.)	Adj[d]	Obs (± 1 s.e.)	Adj	Obs (± 1 s.e.)	Adj	Obs (± 1 s.e.)	Adj	Obs	Adj
3	302.36 ± 5.27		361.38 ± 5.29		344.00 ± 8.25		366.66 ± 4.71			
1	275.36 ± 4.68	300.80	324.85 ± 4.08	306.50	304.50 ± 5.55	306.47	337.00 ± 3.49	314.74	**	*
2	304.14 ± 5.10	335.02	358.00 ± 4.89	335.75	329.37 ± 7.26	331.77	361.83 ± 4.40	334.82	**	n.s.
4	92.21 ± 1.53	100.47	103.08 ± 1.91	97.13	96.75 ± 1.81	97.39	105.50 ± 2.09	98.28	**	n.s.
5	66.14 ± 1.08	72.07	75.23 ± 2.02	70.96	71.87 ± 1.43	72.33	77.50 ± 0.76	72.31	**	n.s.
6	23.07 ± 0.79	26.14	29.93 ± 0.85	27.71	26.62 ± 0.82	26.86	30.00 ± 0.96	27.31	**	n.s.
7	165.57 ± 4.58	181.39	196.54 ± 4.21	185.14	186.25 ± 2.72	187.48	208.67 ± 4.52	194.83	**	n.s.
8	107.21 ± 1.87	115.38	119.61 ± 1.77	113.73	115.37 ± 1.75	116.01	119.17 ± 1.35	112.02	**	n.s.
9	74.86 ± 2.28	84.01	87.23 ± 1.94	80.63	82.12 ± 3.76	82.83	93.83 ± 3.02	85.83	**	n.s.

[a] See Table 1 for the list of characters. – [b] See 'Material and Methods' for the description of the populations. – [c] Observed means. – [d] The adjusted means were computed following the formula; $\hat{y}i = \bar{y}i - b_j(\bar{X}_i - \bar{\bar{X}})$, where: $\hat{y}i$ is the adjusted mean; $\bar{y}i$ is the correspondent observed mean; b_j is the regression coefficient obtained through analysis of covariance and correspondent to the j character; $\bar{X}i$ is the mean of the character 3 for the i group; $\bar{\bar{X}}$ is the general mean of the character 3 (from: SNEDECOR and COCKRAN 1967). – ** $p \leq 0.01$; * $p \leq 0.05$; n.s. = not significant

following NEI (1972) and ROGERS (1972). These distances were clustered through an UPGMA procedure (SNEATH and SOKAL 1973) in order to obtain a phenogram depicting the probable genetic relationships among the groups.

Results

Analysis of covariance

Mean values of the 9 skull characters (males only) and the corresponding adjusted means are shown in Tab. 3. The analysis of variance of the observed means shows highly significant differences for all the characters, among the 4 wild boar groups ($p \leq 0.01$). The Sardinian population is particularly well separated from the Italian CCP one. Its dimensions appear larger than the present (CSR) as well as the old (CMAJ) Maremma populations. After analysis of covariance between the median superior length (considered as independent variable and as a good extimator of the size of the skull) and all the other variables (supposed depending from size) a set of adjusted means is obtained. The mean differences among the 4 groups appear to be very small and not statistically significant, character n. 1 excluded ($P \leq 0.05$), when the size factor is removed.

The "F"-test of the adjusted means is a test of parallelism among the regression lines of each variable on the size of the skull. We can observe that, size factor excluded, no significant dimensional difference among groups remains to suggest possible allometric variations. The difference between the Sardinia and the CCP groups is explained by the significance of the character n. 1 mean difference between the 4 groups.

PCA and CA computed with the observed values

About the 90 % of the total variability is explained by the two principal components PC-I and PC-II. The plotting of the male sample scores shows clear elliptic and elongated clusters (Fig. 2A) suggesting a high correlation among characters due to the effect of size variation (SNEATH and SOKAL

1973). All the characters show similar loadings on PC-I, behaving as they were the expression of a single size factor. Groups overlap each other along a linear sequence following size variation. Shape differences, expressed through some inverse correlations between lengths (characters n. 1, n. 2 and n. 3) and widths (characters n. 4 and n. 5), come out from the eigenvectors plot on PC-II. This principal component explains only the 4,4 % of the total variability and therefore it cannot produce any discrete cluster on PC-II (Fig. 2A). Similar results came out from CA, the order of the groups being the same PCA produces, while a better discrimination among them is evident. The Sardinian and the CCP groups are fairly separated at the ends, while CSR and CMAJ are near the middle of the distribution, with large overlaps (Fig. 2C). The separation between the Italian and the Sardinian populations appears rather clear.

Both PCA and CA give similar results by computing the male as well as the female values (Fig. 2B and 2D). (Measures on CMAJ females not available). The Sardinia females appear very clearly separated from the CSR and CCP ones, completely overlapping between them. The PC-I eigenvector shows a similar loading structure both in males and in females.

PCA and CA of the Logs and Ratios

PCA computed using the Log-transformed data produce distributions similar to those obtained from the observed values (Fig. 3A; Fig. 3B). The percent of explained variance and the structure of the eigenvectors remain also unchanged, both in males and in females, showing the noninfluent effect of sampling variance on multivariate outputs. CA of these data cannot produce any output being the determinant of the within groups matrix too small to give a possibility of discrimination.

PCA computed from the Ratio-transformed data show the effect of the dramatic reduction of variability, being the groups almost totally overlapping (Fig. 3C; 3D). While in males the Sardinian group separates a little from the Italian samples, in females the wide separation observed using the observed and the Log-transformed data, disappears completely. Moreover, the total phenotypic variability is distributed among several principal components. Using the observed and the Log-transformed data, PC-I explains about the 85 % of the variability and PC-I and PC-II together explain more than the 90 %. Working with the Ratio-transformed data we obtain a PC-I explaining only the 37 % of the total variability and we must cumulate the first six PCs to exceed the 90 %.

The eigenvectors structure shows possible allometric differences among the samples, but the residual variability after the data transformation is so small not to allow any discrimination.

CA computed from the Ratio-transformed data does not produce any output because of the great reduction of variability. The removal of the variation linked to different skull size, make impossible any multivariate discrimination among groups.

PCA and CA of the adjusted values

Adjusting the data in order to remove the effect of the size of the skull, we obtain clusters, computed through PCA, showing a spherical shape within the first two PC (Fig. 4A). the elliptic shape of the clusters is lost because of the data transformation: the correlation of each character with the size of the skull has been removed. The 4 groups now clearly overlap, especially if projected on PC-I. PCA produces PC-I and PC-II explaining the 50 % of the total phenotypic variability. These first two components are roughly equivalents (PC-I = 33 %, PC-II = 21 %). Without size effect the residual phenotypic variability is largely distributed among the principal components. The eigenvectors structure is similar both on PC-I and on PC-II and it expresses shape differences within the samples.

CA computed on the adjusted values is once again more efficient in discriminating among groups (Fig. 4B). Some possible elements of allometric variation allow a small

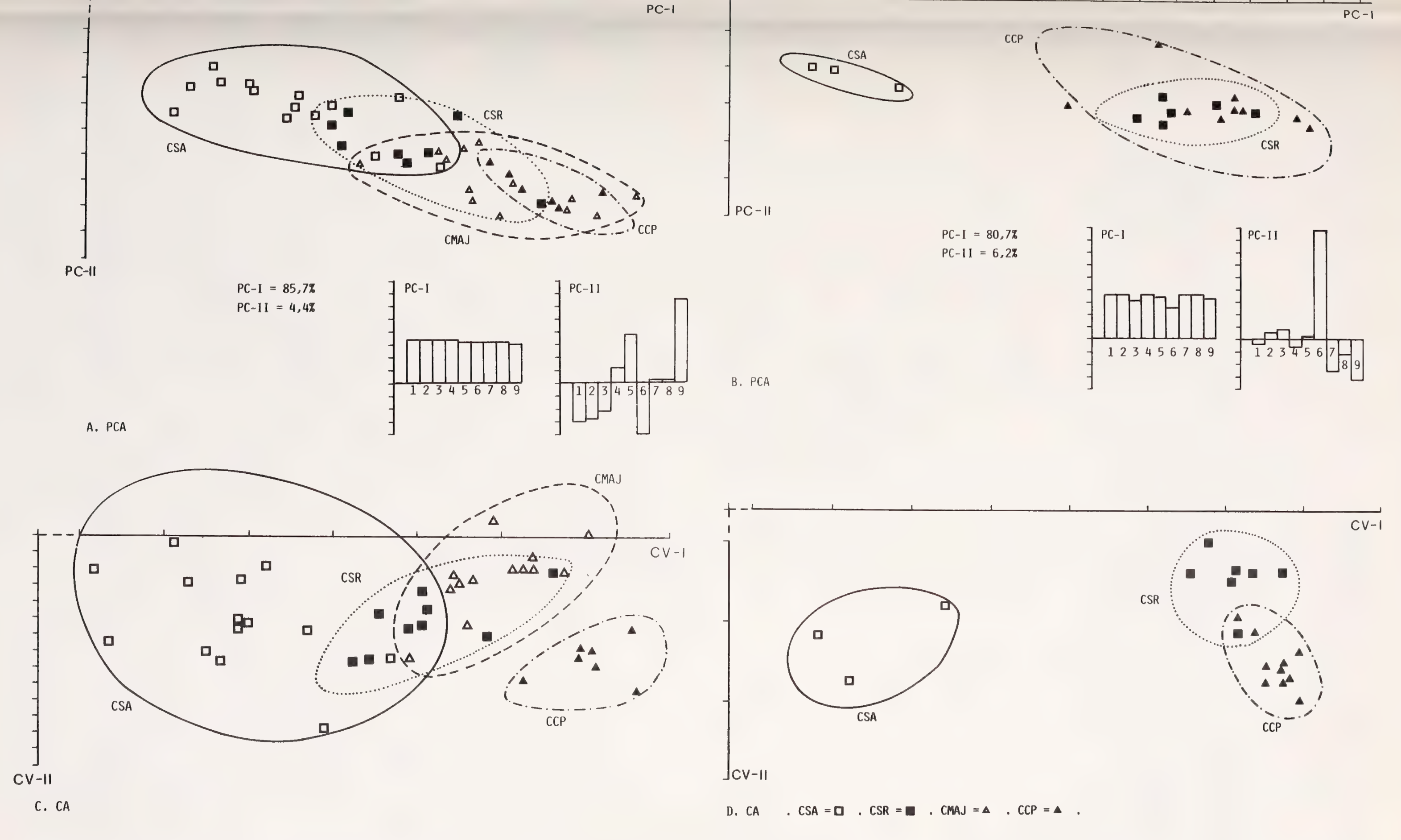


Fig. 2. Multivariate analyses of the observed values A: PCA ♂♂; B: PCA ♀♀; C: CA ♂♂; D: CA ♀♀. PC-I = first Principal Component. PC-II = second Principal Component. For the list of the sampled populations and of the craniometric characters, see “Material and methods”

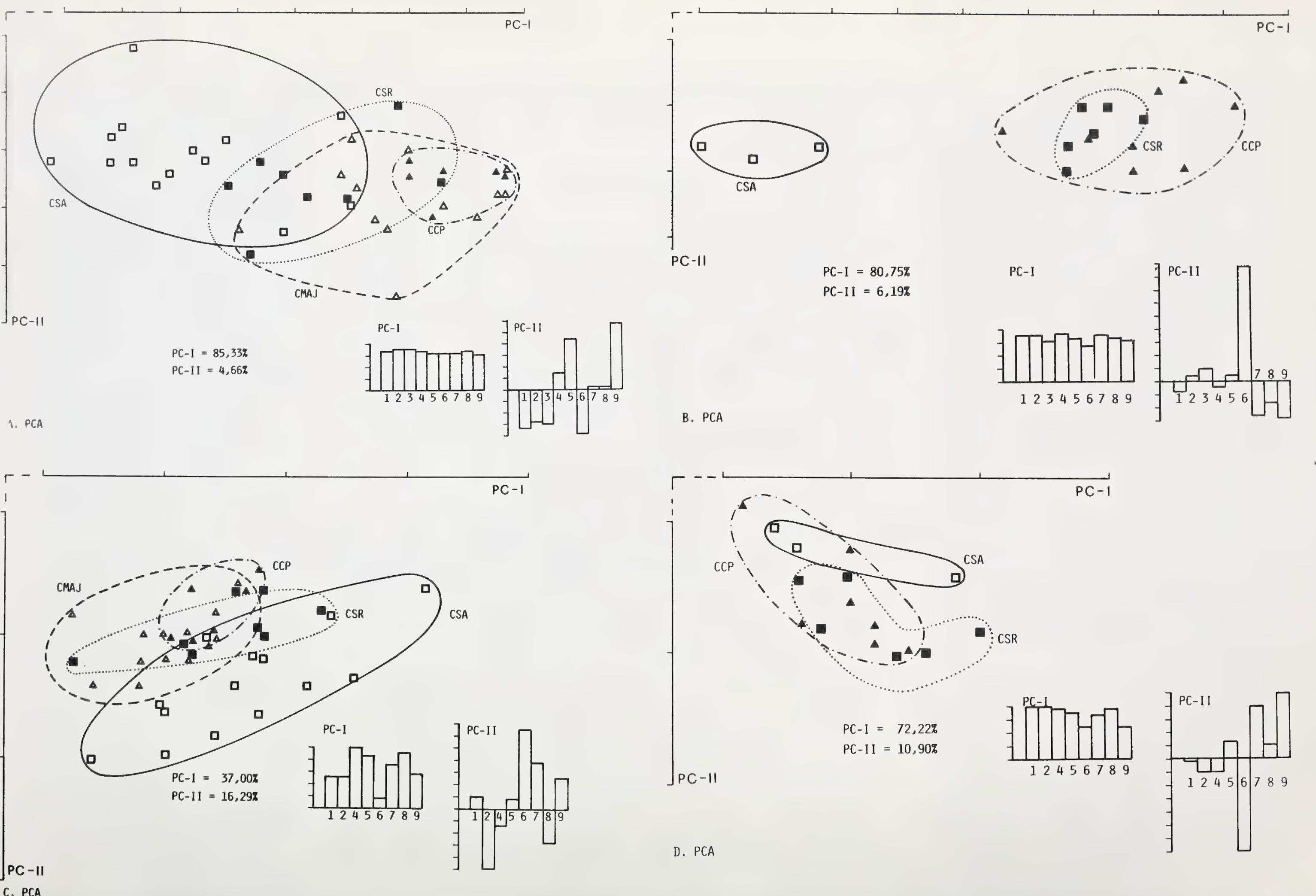


Fig. 3. Multivariate analyses of the Log- and Ratio-transformed values. A: PCA ♂♂ Log-transformed; B: PCA ♀♀ Log-transformed; C = PCA ♂♂ Ratio-transformed; D: PCA ♀♀ Ratio-transformed. PC-I, PC-II, sampled populations and characters as in Fig. 2.

separation of the Sardinia group. The portion of the total variability explained by allometry is however very small. The analysis of females produces similar results (not shown).

Electrophoresis

The listing of the polymorphic loci for each group, with the allele frequencies and their standard errors, the values of the observed heterozygosities and the χ^2 test of agreement with the expected Hardy-Weinberg heterozygosities, is shown in Table 4.

In the wild boar samples there are 4 polymorphic loci (PGI, PGM-2, LAP-Rbc and Tf), while in the domestic pigs there are only 3 polymorphic loci (PGI, 6PGD, Tf). These polymorphisms are shared among groups, although several groups have been checked

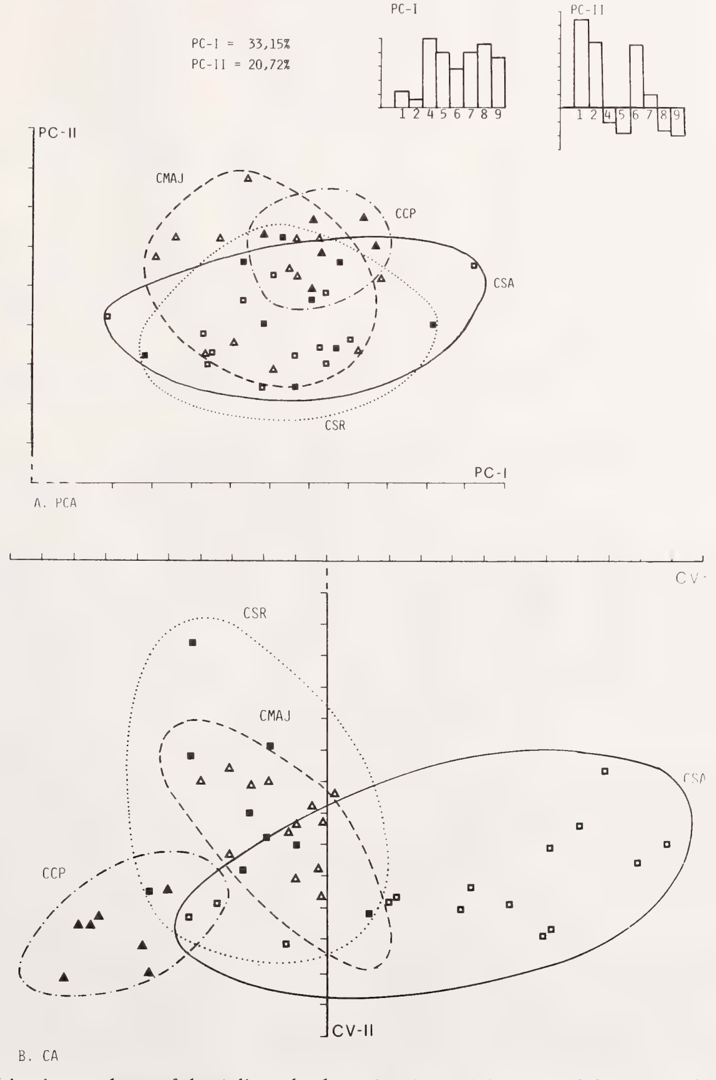


Fig. 4. Multivariate analyses of the Adjusted values. A = PCA ♂♂. B: CA ♀♀. PC-I, PC-II, sampled populations and characters as in Fig. 2

Table 4. **List of polymorphic loci, allele frequencies with their standard errors (s.e.), observed eterozygosities (H_L) and χ^2 test**

Population	Locus	Allele frequencies a	b	s.e.	H_L	χ^2	n
CSR	PGI	0.032	0.968	0.012	0.062	n.s.	109
	PGM-2	0.023	0.977	0.010	0.045	n.s.	109
	LAP-Rbc	0.014	0.986	0.010	0.028	n.s.	71
	Tf	0.250	0.750	0.056	0.375	**	30
CCP	PGI	0.171	0.829	0.045	0.284	n.s.	35
	PGM-2	0.071	0.929	0.031	0.133	n.s.	35
	LAP-Rbc	0.057	0.943	0.028	0.107	n.s.	35
	Tf	0.324	0.676	0.080	0.438	*	17
CSA	PGI	0.056	0.944	0.054	0.105	n.s.	9
	Tf	0.167	0.833	0.088	0.278	n.s.	9
CPM	PGI	0.500	0.500	0.063	0.500	n.s.	31
	Tf	0.391	0.609	0.061	0.476	n.s.	31
CFR	PGI	0.033	0.967	0.033	0.064	n.s.	15
	PGM-2	0.067	0.933	0.045	0.124	n.s.	15
	Tf	0.286	0.714	0.085	0.408	n.s.	14
MBO	PGI	0.309	0.691	0.048	0.427	*	47
	6PGD	0.596	0.404	0.051	0.482	n.s.	47
	Tf	0.063	0.938	0.027	0.117	n.s.	47
MSA	PGI	0.095	0.905	0.045	0.172	n.s.	21

* = $p \leq 0.05$; ** = $p \leq 0.01$; n.s. = not significant; n = sample size

Table 5. **Genetic variability within population**

Population	Ne	P	H
CSR	1.24	0.14	0.015
CCP	1.36	0.14	0.029
CSA	1.25	0.06	0.012
CPM	1.98	0.06	0.030
CFR	1.67	0.10	0.005
MBO	1.60	0.10	0.030
MSA	1.21	0.03	0.005
Wild boars		0.12	0.021
Domestic pigs		0.09	0.015

Ne = effective allele number at the polymorphic loci;
P = percent of polymorphism;
H = mean heterozygosity over all the studied loci

monomorphic at some of these loci, so the effective allele numbers (Ne) as well as the percent of polymorphism (P), are variable among groups (Table 5).

The NEI's genetic identities (I), and distances (D) among groups are shown in Table 6. The values of Is are very high, therefore the Ds among groups are very small (ROGERS' values are highly correlated to the NEI's D values, so they are not shown here).

The NEI's Ds are clustered through an UPGMA procedure and they are shown in Fig. 5 (using the ROGERS' S the same dendrogram is obtained). A first cluster includes the three continental populations: CFR, CSR and CCP, linked together by small values of D. Well separated from this cluster there is a second cluster including the Sardinia populations. The Sardinia domestic pigs (MSA) and the Sardinia wild boars (CSA) are closely linked together, but fairly away from the continental Italian groups. The crossed population living in the Natural Park of Maremma (CPM), is well separated between the wild boar cluster and the Landrace domestic (MBO) lineage.

Table 6. **Genetic variability among populations**

Populations	CSR	CCP	CSA	CPM	CFR	MBO	MSA
CSR		0.0009	0.0006	0.0074	0.0001	0.0086	0.0020
CCP	0.999		0.0020	0.0038	0.0007	0.0081	0.0036
CSA	0.999	0.998		0.0085	0.0011	0.0071	0.0004
CPM	0.993	0.996	0.992		0.0073	0.0097	0.0097
CFR	1.000	0.999	0.999	0.993		0.0091	0.0027
MBO	0.991	0.992	0.993	0.990	0.991		0.0065
MSA	0.998	0.996	1.000	0.990	0.997	0.994	

Nei's genetic distances D (upper triangular matrix); Nei's genetic identities I (lower triangular matrix)

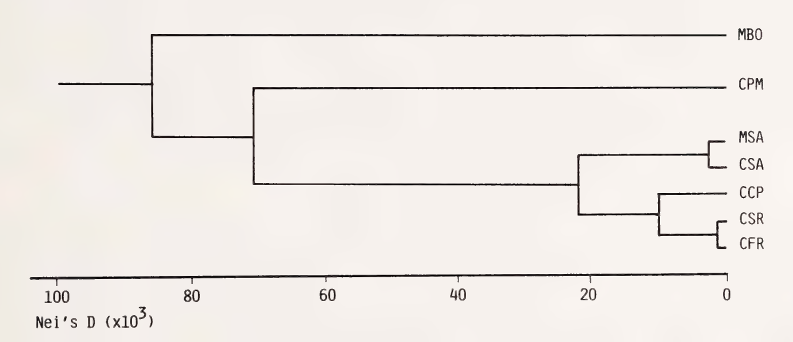


Fig. 5. UPGMA dendrogram showing possible relationships among populations computed from NEI's D values

Discussion

Morphometrics

The 4 populations we have studied were characterized through 9 skull measures the mean values of which proved significantly different. The adjusted mean values obtained after the removal of the size effect, appear not to be significantly different. So, size variation apart, these populations are not distinguishable from a univariate point of view. Multivariate analyses confirm this indication: the main factor of variation among population is a size factor. PCA computed using the observed values produces an elliptic swarm of the sample scores with a poor clustering of each populations that overlaps and dispose themselves following a linear sequence reflecting size differences.

Log-transformation of the observed values produces similar multivariate results. Ratio-transformed data produces a great reduction in variability. The population clusters show circular shape and the overlaps are wide. The prevalence of a dimensional factor in the discrimination among groups is supported by an analysis of the eigenvectors structure. PCA of the observed values gives a PC-I explaining about the 90 % of the total variability; all the characters on PC-I show similar loadings. The structure of the loadings on PC-II suggests shape differences, but the explained variability is so small not to allow any detection of clusters. PCA of the ratio transformed data distributes about the 90 % of the total phenotypic variability among the first six principal components and the loadings show shape differences on PC-I too. The main factor of variation among these 4 groups is a size factor expressed, in this case, through the median length of the skull.

Such a factor is correlated to all the skull characters we have studied, and it explains the greatest portion of the total variability. This factor is removed by adjusting the data after

the regression analysis, i. e. the variation explained through the size differences between populations is removed, so that any difference between them disappears and the residual variability is distributed on more, allometrically structured, principal components. This variability is, anyway, not great enough to discriminate among the groups.

CA model is designed to allow a maximisation of the morphometric distances among groups, so that they are discriminated better than PCA did. A better separation of the Sardinian sample on one side and of the CCP sample on the other side, is apparent.

The huge reduction of variability, within as well as between groups, following the Log- and Ratio-transformation, produces determinants of the within groups matrices so small that CA cannot give any output. No discrimination among groups is then possible.

Computing the adjusted data PCA cannot discriminate any population, while CA shows a permanent fair separation of the Sardinian group. If size differences among populations have been removed and the residual differences are due to allometric variations, we can conclude these are quantitatively very small and may fairly discriminate only a portion of the Sardinian population. The continental Italian samples overlap incompletely. The CCP sample, showing a large absolute size, plots rather apart also using adjusted data. It seems possible that small sample size and possible non-randomness in the choice of the specimens granted for study may have biased the results.

Electrophoresis

The results showed in the present work are among the few electrophoretic analyses on wild boar populations in Western Europe (Hartl and Csaikl 1987), while extensive research has been performed on several domestic pig breeds and on some wild populations in Asia and Eastern Europe (Tanaka et al. 1983; Schmid et al. 1980).

All loci we have found to be polymorphic in the wild boar, have been described as polymorphic in a wide number of domestic pig breeds (Ollivier and Sellier 1982; Franceschi and Ollivier 1981) as well as in the few studied wild boar populations (Smith et al. 1980; Hartl and Csaikl 1987).

A previously undescribed electrophoretic variation at the LAP-Rbc locus (Randi et al. 1986), was found only in the Maremma populations (CCP and CSR samples). This variant has not been detected in the Sardinian and in the French samples we have studied. This locus could be a genetic marker useful to detect differences between domestic and wild pig and could, moreover, have a narrow geographic diffusion. However, because no data was found in literature about this locus and because of the small size of some of our samples, it seems premature to draw any relevant conclusion.

The mean values of P and H we have computed for wild boars fall within the range estimated for large mammals (Nevo 1984). It is noteworthy that almost all the studied domestic pig breeds have been found polymorphic at the locus 6PGD (Rasmussen 1983; Oishi and Abe 1975; Dinklage 1969; Widar et al. 1975) while all the wild boar samples we have studied appear to be monomorphic. The polymorphism at the locus 6 PGD in the domestic pig is attributable to two alleles both present, almost in all breeds, at nearly intermediate frequencies so that even in a small sample it easily should be detectable. Moreover the presence of such a polymorphism is noteworthy in the Landrace breed we analyzed, while the Sardinian, native, unimproved domestic pigs appear to be monomorphic. A deeper discussion may start from the results published by Smith et al. (1980) on some electrophoretic analyses of samples from populations of domestic and feral pigs and of European wild boars that were introduced to the United States. The feral populations are the offspring of free ranging domestic pigs living in the Savannah River region before 1952, so they are feral since only a few generations. Another population on the Ossabaw Island is feral since about 400 years. In the Great Smoky Mountains National Park lives a population at least partly descending from a stock of introduced European wild boars.

All the domestic pig breeeds have been found polymorphic at the locus 6PGD, as well as the local domestic stock, with intermediate allele frequencies. The Savannah River feral population has been found polymorphic with practically the same allele frequencies of the domestic ones, while the Ossabaw ancient feral pigs show monomorphic the locus 6PGD. The Smoky Mountains wild boars are also monomorphic. Moreover a sample of 145 wild boars from four populations in Austria has been found monomorphic at this locus (Hartl and Csaikl 1987).

Two possible interpretations are suggested by these data:

1. Only one of the two alleles at the locus 6PGD is maintained in the wild populations. This locus is forced to be monomorphic because one allele is selected against by its own low fitness or, more probably, because of linkage with other unfavourable traits in natural environment. On the contrary this polymorphism is compatible with domestic life or, possibly, it is maintained in consequence of the artificial selection the breeders practice on the domestic breeds.
2. The domestic pig breeds intensively reared and genetically improved have an hybrid origin, deriving from European domestic breeds crossed with Asian breeds. While native European domestic breeds possibly derived from groups of European wild boars, native Asiatic breeds derived from Eastern wild populations (Epstein and Bichard 1984). Following the hypothesis that the Western wild and native domestic populations are monomorphic at the locus 6PGD, we can then suppose that some Eastern populations are polymorphic or monomorphic for the alternative allele so that the crossings performed to obtain the first improved genotypes can have produced this polymorphism at the locus 6PGD.

We must note that our CSR wild boar population, heavily interbred with domestic pigs since about 140 years, now shows an electrophoretic genetic structure similar to the other continental wild boar populations.

Native Sadinian domestic pigs appear to be monomorphic at the locus 6PGD and genetically very similar to the Sardinian wild boars. Moreover we can point out that our CPM sample is monomorphic at the locus 6PGD despite the recent heavy interbreeding with native domestic pigs belonging to the Cinta Senese breed (probably monomorphic; unpubl. observations).

These two hypotheses are of course not mutually exclusive: it is conceivable that the Eastern wild populations have a genetic structure dissimilar from the Western ones. Some indications are deducible from literature (Tanaka et al. 1983) but we do not know any published data on the locus 6PGD for Asiatic populations. These studies clearly state that Asian native breeds are genetically different from the improved European and American ones. If the present improved breeds have an hybrid origin their genome will bear the tracks of the parental populations. Furthermore one may think that, within the genetic background of the Western populations and within the environmental conditions the European wild boars live, the "Eastern" allele is selected against and then the locus 6PGD is driven toward monomorphism.

Anyway this locus seems to be very interesting to detect the genetic status of the European wild boar populations. Populations showing wild phenotypes but polymorphic at the locus 6PGD should be heavily suspected to be genetically polluted with improved domestic genomes. It might of course be very useful to extend the analysis and study other European native breeds and the Eastern subspecies *Sus scrofa vittatus* as well, in order to verify the genetic structure of the locus 6PGD.

In some few cases the observed heterozygosities do not agree with these expected under the equilibrium of Hardy-Weinberg (Table 4). The PGI case in the MBO sample may be the consequence of industrial rearing techniques: the breeding scheme possibly employed for the genetic improvement could have produced the observed disequilibrium. It is well known that the PGI locus is linked to the halotane locus (Rasmussen 1983). In the

domestic pig the locus PGI is polymorphic with two alleles, "a" and "b", of which "b" is always the more frequent one. The "b/b" genotype is linked with the halotane susceptibility, while the "a/a" and "a/b" genotypes are linked with the halotane resistance. In our MBO sample the frequency of "a" is clearly greater than in the wild boar populations, and the expected HARDY-WEINBERG genetic frequencies show an excess of observed alleles "a": the allele "b" could have been selected against. The Tf case in the CSR and CCP samples might be the consequence of having analyzed some hemolyzed serum samples in which the visual identification of the Tf bands may be confounded by the presence of Haptoglobin-Haemoglobin complexes. In all the other cases the agreement with the expected HARDY-WEINBERG allele frequencies is good.

The UPGMA dendrogram computed from the NEI's D matrix clearly shows a cluster including the two continental Italian and the South France populations; a second cluster including the Sardinian wild and domestic pigs and, well apart, the domestic Landrace breed and the crossed wild population living in the Parco della Maremma. In this population the recent heavy crossing with a native domestic pig breed (Cinta Senese), has clearly produced genotypes rather different from the genotypes of the wild populations living in the same range (Tuscany Maremma). The locus PGI, polymorphic in all the studied samples but generally with the "b" allele showing a high frequence near or a beyond the 90 % in the wild boar populations, seems to be a marker. In the CPM sample two alleles are present at this locus, both at the same frequency (0.50). In the domestic sample MBO the frequency of "b" is lower (0.69) than in any wild population. The Maremma Natural Park wild boars show a high phenotypic variability, and a selective program is now carried out with the aim to remove the morphologically abnormal specimens (BOSCHI 1984).

The Sardinian native domestic pigs and wild boars appear genetically very similar, suggesting a possible common origin and/or a continuous gene flow. The origin of the Sardinian wild boar is still debated (APOLLONIO et al., in press). It could be a wild continental population that became isolated or a domestic one, brought in by man in the past, which became feral. The native domestic stock could be the descendant of the original domestic population brought in by man, or it could have been tamed directly on the island starting from some wild individuals. Anyway the traditional rearing of the pigs in semi-wild conditions is still widely practised in Sardinia, so that an extensive gene flow is possible between the two populations. A strong genetic similarity is then understandable.

From the analysis of the craniometric and electrophoretic data we suggest that the Sardinian subspecies *S. s. meridionalis* should be maintained. The body size of the Sardinian wild boars is much smaller than any other Italian populations, the structure of the skull shows possible allometric differences in respect to the old and recent Maremma populations. The Sardinian lineage is fairly well electrophoretically separated from the continental cluster, including the Maremma and the French populations.

The present Maremma and France populations show a strong genetic similarity. Gene flow across these populations has probably never been interrupted for a time long enough to allow genetic divergence. The hypothesis that the size differences between the Western European populations have a prevalent environmental base is then supported. The environmental modifications produced by human activities in connection with demographic reductions European wild boars formerly have experienced certainly have originated populations reproductively isolated, but such an isolation has probably concerned populations previously not differentiated and it has not enough been prolonged to determine genetic divergence.

Craniometric and electrophoretic data suggest the opportunity to suppress the subspecies *S. s. majori* and to consider all the present Italian populations as belonging to the nominate form *Sus scrofa scrofa*.

Acknowledgements

We wish to acknowledge the help of the Director of the San Rossore preserve, Dr. A. DE MARINIS; the Director of the Castelporziano preserve, Dr. G. EMILIANI; the Director of the Parco Nazionale della Maremma, Dr. I. BOSCHI. A. AZZAROLI, G. DELITALA, A. GIOVANNINI, F. SPITZ, L. TINELLI, the Natural History Museums of Milan, Florence, Turin, Genua, the Museum of the National Institute of Wildlife Biology, kindly provided us with material for this study. L. RIGACCI and Mrs. D. MATTEUCCI helped us in the laboratory analysis. Mrs. M. L. ROMAGNOLI and M. SPISNI carefully typed the manuscript and prepared the figures. We wish to thank particularly F. SPITZ and S. LOVARI who kindly revised a first draft of the manuscript.

Zusammenfassung

Zur Systematik einiger italienischer Wildschweinpopulationen (Sus scrofa L.). Eine craniometrische und elektrophoretische Analyse

Zur Klärung taxonomischer Beziehungen und zur Überprüfung der Validität der beiden italienischen Unterarten *Sus scrofa majori* De Beaux und Festa, 1927 und *S. s. meridionalis* Major, 1883 wurden craniometrische und elektrophoretische Untersuchungen an italienischen und französischen Wildschweinpopulationen sowie an zwei verschiedenen Hausschweinrassen durchgeführt.

Neun Schädelmaße an 41 Wildschweinen (alte und rezente Populationen von Maremma und Sardinien-Populationen) wurden mittels univariater und multivariater Analyse ausgewertet. Stichproben von 200 Wildschweinen (Populationen aus Maremma, Sardinien, und dem südwestlichen Frankreich) und zusätzlich 68 Hausschweinen wurden ferner elektrophoretisch bearbeitet.

Die statistische Analyse ergab, daß die sardinische Population von den sich überlagernden Clustern der kontinentalen italienischen Populationen getrennt war. Die multivariate Analyse der bearbeiteten Daten zeigte hingegen eine allgemeine Überlappung der Gruppen. Die morphometrischen Unterschiede zwischen italienischen, wie zwischen west-paläarktischen Wildschweinpopulationen werden hauptsächlich durch den beeinflussenden Faktor Körpergröße erklärbar.

Die elektrophoretischen Untersuchungen haben genetische Besonderheiten der Loci LAB-rbc und 6 PGD ergeben. Ein Dendrogramm, erstellt an Abständen nach NEI, zeigt ein Cluster für die italienische Maremma- und die französische Population. Deutlich getrennt davon ist ein zweites Cluster für Sardinische Wild- und Hausschweine.

Abgesetzt davon wiederum erscheinen die untersuchten Hausschweine der Landrasse und auch eine Wildschweinpopulation, in die seit kurzer Zeit Hausschweine eingekreuzt sind.

Da die italienische Maremma-Population entsprechend unseren Befunden den westeuropäischen *Sus scrofa* zugeordnet werden müssen, erscheint ihr Unterarten-Status nicht valid und sollte beseitigt werden. Das sardinische Wildschwein ist demgegenüber sowohl morphologisch als auch elektrophoretisch gut characterisiert. Deshalb sollte diese Unterart weiterhin als gültig betrachtet werden.

References

APOLLONIO, M.; RANDI, E.; TOSO, S. (1987): The systematics of the wild boar (*Sus scrofa* L.) in Italy. Boll. Zool. (in press).

BOSCHI, I. (1984): Amélioration d'une population de sanglier dans le Parc Natural de la Maremme. Interventions. Premiers résultats. In: Symposium International sur le sanglier. Ed. by F. SPITZ and D. PEPIN. Tolouse: INRA. pp. 169–172.

DAVIS, B. J. (1964): Disc electrophoresis. II. Method and application to human serum proteins. Ann. N.Y. Acad. Sci. **121**, 404–427.

DE BEAUX, O.; FESTA, E. (1927): La ricomparsa del Cinghiale nell'Italia settentrionale-occidentale. Mem. Soc. It. Scienze Nat. e Mus. Civ. St. Nat., Milano, III, 263–322.

DINKLAGE, H. (1969): 6-phosphogluconat-dehydrogenase Polymorphismus beim Schwein. Züchtungskunde **41**, 326–330.

EPSTEIN, H.; BICHARD, M. (1984): Pig. In: Evolution of domesticated animals. Ed. by L. MASON. New York: Longman. pp. 145–162.

FERGUSON, A. (1980): Biochemical Systematics and Evolution. New York: Wiley.

FRANCESCHI, P. F.; OLLIVIER, L. (1981): Frequences de quelques gènes importants dans les populations porcines. Z. Tierzüchtg. Züchtgsbiol. **98**, 176–186.

GRUNBAUM, B. W. (Ed.) (1981): Handbook for forensic individualization of human blood and bloodstains. Göttingen: Sartorius GmbH.

HARRIS, H.; HOPKINSON, D. A. (1976): Handbook of enzyme electrophoresis in human genetics. Amsterdam: North Holland Publ. Co.

HARTL, G. B.; CSAIKL, F. (1987): Genetic variability and differentiation in wild boars (*Sus scrofa ferus* L.); Comparison of isolated populations. J. Mammalogy **68**, 119–125.

MAJOR, F. (1883): L'origine delle faune delle nostre isole. Atti Soc. Tosc. Scienze Nat. Pisa. Processi verbali III, 1881–1883, 119–122.
MAJOR, F. (1885): I cinghiali dell'Italia. Studi craniologici. Atti Soc. Tosc. Scienze Nat. Pisa. Memorie VI, **2**, 346–362.
MILLER, G. S. (1912): Catalogue of Mammals of Western Europe in the British Museum. London. pp. 956–962.
MORRISON, D. F. (1967): Multivariate statistical methods. New York: McGraw Hill.
NEI, M. (1972): Genetic distances between populations. Am. Nat. **106**, 283–292.
NEVO, E.; BEILES, A.; BEN-SHOLMO, R. (1984): The evolutionary significance of genetic diversity: Ecological, demografic and life history correlates. In: Lecture Notes in Biomathematics. Vol. 53. Ed. by G. S. MANI. Berlin: Springer. pp. 13–213.
OISHI, T.; ABE, T. (1979): Polymorphism of PHI, 6PGD, PGM and ADA enzymes in porcine red cells. Bull. Nat. Inst. Anim. Ind. **35**, 9–18.
OLLIVIER, L.; SELLIER, P. (1982): Pig genetics: a review. An. Genet. Sel. Anim. **14**, 481–544.
RANDI, E.; APOLLONIO, M.; TOSO, S. (1986): Electrophoretic polymorphism of erythrocyte leucine aminopeptidase in the wild boar, *Sus scrofa*. An. Genet. **17**, 359–362.
RASMUSSEN, B. A. (1983): Isozymes in Swine breeding. In: Isozymes: Current Topics in Biological and Medical Research. Vol. 11. Ed. by M. C. RATTAZZI, J. G. SCANDALIOS, G. S. WHITT. New York: A. Liss. pp. 249–268.
ROGERS, J. S. (1972): Measures of genetic similarity and genetic distance. Univ. Texas Publ. **7213**, 145–153.
SCHMID, D. O.; SUZUKI, S. (1980): Animal blood group research; today and future in West Germany and Japan (A review). J. Agric. Science, Tokyo, **25**, 91–112.
SELANDER, R. K.; SMITH, M. H.; YANG, S. Y.; JOHNSON, W. E.; GENTRY, J. B. (1971): Biochemical polymorphism and systematics in the genus *Peromyscus*. In: Studies in genetics VI. Univ. Texas Publ. **7103**, 49–90.
SMITH, M. W.; SMITH, M. H.; BRISBIN, I. I., JR. (1980): Genetic variability and domestication in swine. J. Mammalogy **61**, 39–45.
SNEATH, P. H. A.; SOKAL, R. R. (1973): Numerical taxonomy. San Francisco: W. H. Freeman and Co.
SNEDECOR, G. W.; COCHRAN, W. G. (1967): Statistical Methods. Ames: Iowa University Press.
STROBEL, P. (1982): Studio comparativo sul teschio del porco delle Mariere. Atti Soc. It. Scienze Nat. Milano **XXV**, 19–85; 163–237.
TANAKA, K.; OISHI, T.; KUROSAWA, Y.; SUZUKI, S. (1983): Genetic relationship among several pig populations in East Asia analyzed by blood groups and serum protein polymorphisms. An. Blood Grps. biochem. Genet. **14**, 191–200.
WIDAR, J.; ANSAY, M.; HANSET, R. (1975): Allozymic variation as an estimate of heterozygosity in Belgian pig breeds. Anim. Blood Grps. biochem. Genet. **6**, 221–234.

Authors' address: Dr. ETTORE RANDI, MARCO APOLLONIO, SILVANO TOSO, Istituto Nazionale di Biologia della Selvaggina, Via Stradelli Guelfi, 23/a, I-40064 Ozzano del'Emilia (BO)

Z. Säugetierkunde 54 (1989) 57–59

ISSN 0044-3468

WISSENSCHAFTLICHE KURZMITTEILUNG

Über *Gerbillus pyramidum* (Rodentia, Gerbillidae) im Sudan

Von S. A. Tawill und J. Niethammer

Department of Zoology, Faculty of Science, University of Khartoum, Sudan, and Zoologisches Institut der Universität Bonn, FRG

Eingang des Ms. 03. 08. 1988

Nach Ellerman und Morrison-Scott (1951) ist *Gerbillus pyramidum* von Palästina durch ganz Nordafrika bis zum Atlantik verbreitet. Dagegen weist Lay (1983) darauf hin, daß topotypische *Gerbillus pyramidum* (Provinz Gizeh in Ägypten) 38 ausnahmslos zweiarmige Chromosomen besitzen, die Chromosomenbilder außerhalb von Ägypten aber sämtlich abweichen. Er folgert, daß die Art daher vorerst nur als in Ägypten vorkommend angegeben werden kann.

Um die Artzugehörigkeit der u. a. von Happold (1967) als *G. pyramidum* bezeichneten Rennmäuse aus der Umgebung von Khartoum im Sudan zu klären, brachte einer von uns (S. A. T.) im Sommer 1987 fünf Exemplare nach Bonn, für die er dort Karyogramme herstellte.

Diese fünf großen *Gerbillus* mit behaarten Sohlen wurden im Juli 1987 bei Khartoum mit Lebendfallen gefangen, anschließend nach Deutschland geflogen und etwa einen Monat später zur Herstellung von Karyogrammen getötet.

Mitotische Metaphasebilder wurden nach der bei Meredith (1969) beschriebenen Methode aus dem Knochenmark des Femur gewonnen. Bälge und Schädel der Tiere wurden in der üblichen Weise präpariert und vermessen.

Karyogramme wurden von vier der fünf Exemplare hergestellt. Sie zeigen 2n = 38 Chromosomen von wenig unterschiedlicher Länge. Alle Chromosomen sind außerdem meta- oder submetazentrisch. Die kleinsten Elemente sind gut halb so lang wie die größten Chromosomen. Wegen der geringen Abstufung in der Größe waren die Geschlechtschromosomen in den Metaphasen nicht identifizierbar. Abgesehen von der Schwanzlänge, die vermutlich unterschiedlich gemessen wurde, stimmen die Maße der fünf Exemplare (Tab. 1) gut mit den von Happold (1967) für *G. pyramidum* von Khartoum angegebenen überein. Dagegen sind sie wesentlich geringer als solche, die Osborn und Helmy (1980) für *G. pyramidum* aus Ägypten aufführen (Tab. 2). In einigen Merkmalen, die *G. pyramidum* in Ägypten zusätzlich von *G. perpallidus, G. gerbillus* und *G. andersoni* unterscheiden, gleichen *G. pyramidum* aus Khartoum solchen aus Kairo: breit endende Nasalia, großes Interparietale, lange Foramina palatina, deutlich verlängerte, dunkle Haare am Schwanzende.

Unsere Karyogramme stimmen völlig mit den von Wassif et al. (1969) für *G. pyramidum* von Abu Rawash und das Fayoum beschriebenen und abgebildeten Karyogrammen überein. Das beweist zwar nicht die Konspezifität mit *G. pyramidum,* schließt aber die Zugehörigkeit zu anderen, morphologisch ähnlichen Arten wie *G. perpallidus, G. gerbillus* und *G. andersoni* aus, die 40 bzw. 42 oder 43 Chromosomen haben. Jedenfalls macht der Befund die Zugehörigkeit der Serie von Khartoum zu *pyramidum* sehr wahrscheinlich.

Bei dieser Gelegenheit sei erwähnt, daß entgegen Lay (1983) auch außerhalb Ägyptens das Vorkommen von *Gerbillus pyramidum* mit 38 Chromosomen erwähnt wurde. Wahr-

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5401-0057 $ 02.50/0

Tabelle 1. **Maße der adulten *Gerbillus pyramidum* bekannten Karyotyps (2n = 38 Chromosomen) von Khartoum/Sudan**

Maß	*Gerbillus* Nr. 1	2	3	4	5
Kopfrumpflänge (Kr)	102	100	121	97	92
Schwanzlänge (Schw)	125	129	149	131	133
Hinterfußlänge (Hf)	28,5	29,0	30,0	28,3	29,0
Ohrlänge (Ohr)	15,0	11,9	16,1	13,1	14,0
Gewicht (Gew)	43	38	55	41	31
Condyloincisivlänge (Cil)	27,2	28,3	33,7	26,8	–
Occipitonasallänge (Onl)	33,3	31,5	34,4	31,2	–
Zygomatikbreite (Zyg)	17,0	16,6	17,6	16,8	–
Hirnkapselbreite (Skb)	15,8	15,0	16,0	16,0	–
Foramen incisivum-Länge (Fori)	5,5	5,3	6,0	5,5	–

Längen in mm, Gewicht in g

Tabelle 2. **Mittelwerte von Maßen adulter *Gerbillus pyramidum***

Maß	A	B	C	D
Kr	122	106	104	102
Schw	153	157	148	133
Hf[1]	35,2	32,5	29,0	29,0
Ohr	18,1	16,0	15,0	14,0
Gew	–	–	44	42
Cil	–	–	28,2	28,8
Onl	35,5	33,3	32,1	32,7
Zyg	19,0	17,2	16,4	17,0
Skb	15,3	14,9	15,6	15,7
Fori	5,9	5,6	5,5	5,5

A = Ägypten *(G. p. pyramidum)*, B = Südost-Ägypten *(G. p. elbaensis)*, C = Provinz Khartoum nach Happold (1967) und D = Khartoum (Tab. 1); Werte unter A und B aus Osborn und Helmy (1980)

[1] Bei Osborn und Helmy (1980) mit Kralle, im Sudan ohne Kralle gemessen; ohne Kralle wären die Hf unter A und B etwa 3 mm kürzer, also 32,2 bzw. 29,5 mm.

man und Gourevitz (1973) zeigen auf ihrer Karte für den Maghreb neben 40 auch 38 Chromosomen, und für Ostafrika (Äthiopien, Somalia) 38 und 39 Chromosomen, letzteres allerdings ohne nähere Angaben. Wahrman und Gourevitz (1973) haben darüber hinaus in ihrer detaillierten Analyse wahrscheinlich gemacht, daß ein ausgedehnter Robertsonscher Polymorphismus die verschiedenen Karyotypen von 38–66 Chromosomen verbinden könnte. Eine Kreuzung zwischen einem ♀ aus Israel mit 66 und einem ♂ aus Algerien mit 40 Chromosomen gelang. Die Fertilität der Hybriden wurde nicht durch Kreuzung nachgewiesen, doch enthielt ein ♂ bei der Sektion normal wirkende Spermien (Wahrman und Zahavi 1958). Die Maße der Serie aus Khartoum sind erheblich geringer als die ägyptischer *G. pyramidum.* Das war zunächst auch ein weiterer Grund, an der Zugehörigkeit zu *G. pyramidum* zu zweifeln. So passen die Maße der Tiere von Khartoum besser zu denen von *G. perpallidus* als von *G. pyramidum* aus Ägypten. Trotzdem stützt auch der morphologische Vergleich die Zugehörigkeit zu *G. pyramidum.* Bereits innerhalb Ägyptens ist eine Tendenz zur Verkleinerung von Nord nach Süd erkennbar. Die südöstliche Unterart *G. p. elbaensis* ist hier nach Osborn und Helmy (1980) kleiner und ungefähr intermediär zwischen *G. pyramidum* aus Nordägypten und von Khartoum. Darüber hinaus sind spezielle, für topotypische *G. pyramidum* charakteristische und diese von ähnlichen Arten im gleichen Gebiet unterscheidende Merkmale bei den Exemplaren von Khartoum wie bei topotypischen *G. pyramidum* ausgebildet.

Für die Abnahme der Körpergröße von Nord nach Süd gibt es bei kleineren Säugetieren im gleichen Gebiet zumindest zwei Parallelen: Nilgrasratten *(Arvicanthis niloticus)* aus dem nördlichen Ägypten sind wesentlich größer als solche aus dem Sudan (Philippi 1988), ebenso Streifenwiesel (*Poecilictis libyca* – Niethammer 1987). Als Ursache könnte man bei

G. pyramidum wie bei *Poecilictis* an regional unterschiedliche Konkurrenz mit verwandten Arten denken: Die Existenz der wenig kleineren Arten *G. perpallidus* und *G. andersoni* im Norden des Areals von *G. pyramidum* könnte hier eine Selektion größerer Formen begünstigt haben.

Literatur

Ellerman, J. R.; Morrison-Scott, T. C. S. (1951): Checklist of Palaearctic and Indian mammals. London: Brit. Mus., Nat. Hist.

Happold, D. C. D. (1967): Guide to the natural history of Khartoum province. 3. Mammals. Sudan Notes Rec. **48,** 111–132.

Lay, D. M. (1983): Taxonomy of the genus *Gerbillus* (Rodentia: Gerbillinae) with comments on the application of generic and subgeneric names and an annotated list of species. Z. Säugetierkunde **48,** 329–354.

Meredith, R. (1969): A simple method for preparing meiotic chromosomes from mammalian testis. Chromosoma **26,** 254–258.

Niethammer, J. (1987): Das Streifenwiesel *(Poecilictis libyca)* im Sudan und seine Gesamtverbreitung. Bonn. zool. Beitr. **38,** 173–182.

Osborn, D. J.; Helmy, I. (1980): The contemporary land mammals of Egypt (including Sinai). Fieldiana Zool. (N. S. 5) Publ. **1309,** 1–579.

Philippi, Th. (1988): Zur innerartlichen Variabilität der Nilgrasratte *Arvicanthis niloticus* (Rodentia, Muridae). Dipl.-Arbeit Bonn.

Wahrman, J.; Gourevitz, P. (1973): Extreme chromosome variability in a colonising rodent. In: Chromosomes Today. Vol. 4. Ed. by Wahrman, J.; Lewis, K. R. New York, Toronto, Jerusalem: John Wiley & Sons.

Wahrman, J.; Zahavi, A. (1958): Cytogenetic analysis of mammalian sibling species by means of hybridization. Proc. X. Internat. Congr. Genetics **2,** 304–305.

Wassif, K.; Lutfy, R. G.; Wassif, S. (1969): Morphological, cytological and taxonomical studies of the rodent genera *Gerbillus* and *Dipodillus* from Egypt. Proc. Egypt. Acad. Sci. **22,** 77–93.

Anschriften der Verfasser: Salah A. Tawill, Department of Zoology, Faculty of Science, University of Khartoum, Sudan, and Prof. Dr. Jochen Niethammer, Zoologisches Institut der Universität Bonn, Poppelsdorfer Schloß, D-5300 Bonn, FRG

BEKANNTMACHUNGEN

Einladung

Die 63. Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde e.V. findet vom Sonntag, dem 10. September, bis Donnerstag, dem 14. September 1989, in Lausanne, Schweiz, statt. Die beiden ersten Tage werden gemeinsam mit der Schweizerischen Gesellschaft für Wildtierforschung organisiert.

Vorläufiges Programm

Sonntag, 10. September:	Anreise	
	19.00 Uhr:	Zwangloser Begrüßungsabend
Montag, 11. September:	9.00 Uhr:	Begrüßung und Eröffnung der Tagung durch den 1. Vorsitzenden im Hörsaal des Collège propédeutique der Universität Lausanne
	9.30 Uhr:	Hauptvortrag zum Schwerpunkt „Wildlife Management und Ökologie", anschließend Kurzvorträge
	17.00 Uhr:	Mitgliederversammlung
	20.00 Uhr:	Filmabend
Dienstag, 12. September:	8.30 Uhr:	Hauptvortrag zum Schwerpunkt „Einsatz der Radiotelemetrie in der Säugetierforschung", anschließend Kurzvorträge
	11.00 Uhr:	Posterdemonstration
	14.30 Uhr:	Kurzvorträge
Mittwoch, 13. September:	8.30 Uhr:	Hauptvortrag zum Schwerpunkt „Endokrinologie und Neurohormone der Säugetiere", anschließend Kurzvorträge
	18.00 Uhr:	Bankett in historischer Stätte der Region Lausanne
Donnerstag, 14. September:	9.00 Uhr:	Exkursion ins Naturschutzgebiet Aletschwald

Alle Interessenten sind zu der Tagung herzlich eingeladen. Neben den angeführten Schwerpunkten werden wir auch diesmal wieder der Vielfalt der säugetierkundlichen Arbeitsgebiete Rechnung tragen (Kurzreferate und Poster-Demonstrationen).

Das Programm mit der Vortragsfolge wird allen Mitgliedern und auf Anfrage auch Nicht-Mitgliedern rechtzeitig vor der Tagung zugesandt. Falls persönliche Einladungen gewünscht werden, wenden Sie sich bitte an den 1. Vorsitzenden, Prof. Dr. E. Kulzer, Institut für Biologie III, Auf der Morgenstelle 28, D-7400 Tübingen.

Bitte melden Sie die Vorträge, die nicht länger als 15 Minuten dauern sollen, und Poster-Demonstrationen möglichst frühzeitig, spätestens bis zum 30. April 1989 (Ausschlußfrist), beim Geschäftsführer der Gesellschaft, Prof. Dr. U. Schmidt, Zoologisches Institut, Poppelsdorfer Schloß, D-5300 Bonn 1, Tel. 02 28/73 54 68, an.

Fragen zum Tagungsort und zur Organisation sind zu richten an: Prof. Dr. P. Vogel, Institut de Zoologie et d'Ecologie, Batiment de Biologie, CH-1015 Lausanne, Schweiz, Tel. 00 41/21/6 92 24 66.

Symposium on Vertebrate Biogeography and Systematics

The "International Symposium on Vertebrate Biogeography and Systematics in the Tropics" will be held from June 5.–8. in 1989 at the Zoologisches Forschungsinstitut und Museum Alexander König in Bonn, FRG. For further information please contact: Dr. Gustav Peters, Zoologisches Forschungsinstitut und Museum Alexander König, Adenauerallee 150–164, D-5300 Bonn 1, FRG.

Gesellschaft für Primatologie

Am 12. Oktober 1988 wurde in Göttingen die *Gesellschaft für Primatologie* gegründet. „Zweck der Gesellschaft ist, sich nachdrücklich für den Schutz der Primaten und den Erhalt ihrer Lebensräume einzusetzen. Die Gesellschaft fördert die Forschung an Primaten und begünstigt die Zusammenarbeit zwischen den Forschern. Sie kann Einrichtungen und Projekte für die Zucht und den Schutz von Primaten fördern, soweit diese die Ziele der Gesellschaft verfolgen." (Aus der Satzung vom 12. 10. 1988.)
Die erste Mitgliederversammlung in Verbindung mit einem wissenschaftlichen Kongreß findet im Herbst 1989 in Göttingen statt. Bei dieser Gelegenheit soll der Vorstand der Gesellschaft gewählt werden.
Auskünfte: Dr. Eberhard Fuchs, Deutsches Primatenzentrum, Kellnerweg 4, D-3400 Göttingen, Tel. (05 51) 3 85 11 30.

BUCHBESPRECHUNGEN

Bryden, M. M.; Harrison, R. (Eds.): **Research on dolphins.** Oxford: Clarendon Press 1986. 478 pp. £ 45,–. ISBN 0-19-857606-4

Cetaceen biology puzzled scientists already in the past and for certain reasons, mainly because of methodologic problems of investigation still does today. This book, with contributions of 32 experienced scientists from Great Britain, USA, Canada, Australia, and China intends to describe some recent research results on dolphins. There are three main parts headlined as anatomy and physiology (9 contributions), dolphins in captivity (3), and dolphins in the oceans (9). In the first chapter integument, brain, mechanoreceptor organs, bronchial morphometry, kidney, and gonads are dealt with, and consequently certain physiological problems concerning adaptation to water environment, diving activity, brain evolution, orientation, osmoregulation, water balance and reproduction are stressed. In the second chapter problems of a dolphin transfer from the wild to the pool, husbandry and training of individuals, and water quality of a pool needed for keeping dolphins are discussed. The studies of the third chapter deal with age and growth of several species in the wild, distribution in the Atlantic Ocean and the Mediterranean Sea, estimations of population sizes, diet, pathology, orientation and navigation, general behaviour in the wild and in captivity, and intraspecific variation in morphometries and colouration.

All in all, this book can be evaluated as a good overview on recent knowledge and problems of research on dolphins. It is well suited to stimulate and inspire interested mammalogists working in many fields.

D. Kruska, Kiel

Mason, C. F.; Mac Donald, S. M.: **Otters.** Ecology and Conservation. Cambridge, London, New York: Cambridge University Press 1986. 236 pp., ISBN 0-521-30716-3

As has already been recognized by mammalogists for a long time and which today is known to great parts of the public as well, European otters have for certain reasons extremely decreased in numbers and distribution areas. This happened in many countries during this century. Consequently especially engaged biologists met in organizations with the aime to change this situation through captive breeding and re-introduction of otter individuals as well as through conservation of otter life habitats. While the works of these people mostly remain of local importance the authors of this book provide a summary of recent knowledge and experience.

Besides a short introduction the book contents five chapters dealing with the special biology of *Lutra lutra*, its distribution and status in Great Britain, the rest of Europe, Asia, and North Africa. Furtheron, the authors discuss what is known about factors that affect otters survival and different methods of this species' conservation. In a concluding chapter the biology and distribution of the world's otter species are presented.

The book is a carefull investigation of the problem at hand. It is written by authors with knowledge of the situation on the British Isles and in Mediterranean countries, and therefore it can be recommended mainly to conservationists but also to mammalogists with broader interests.

D. Kruska, Kiel

Warhol, A.; Benirschke, K.: **Vanishing animals.** New York, Berlin, Heidelberg, London, Paris, Tokyo: Springer-Verlag 1986. 99 S., 42 Abb., DM 120,–. ISBN 3-540-96410-X

Den Kern des Bandes bilden 16 farbige Drucke von Tierdarstellungen (silkscreen over collage) und zwei Schwarzweiß-Skizzen durch Andy Warhol, die von dem Pathologen und früheren wissenschaftlichen Leiter des San Diego-Zoos Kurt Benirschke kommentiert werden. Neben einigen Vögeln, Reptilien und Schmetterlingen werden acht Säugetierarten und nicht näher spezifizierte Fledermäuse dargestellt und besprochen: Przewalski-Pferd, La Plata-Delphin, Gürtelmaus, Chaco-Pekari *(Catagonus wagneri)*, Okapi, Sumatra-Nashorn, Kleideraffe und Sömmering-Gazelle. An den Bildern werden wohl viele ihre Freude haben. Der begleitende Text plaudert über die abgebildeten Arten und ihre nächsten Verwandten, ihre Verbreitung und Lebensweise, die Schwierigkeiten der Haltung in zoologischen Gärten, den Bestand und seine Bedrohung. Er liest sich gut, ist informativ und zutreffend und zeugt von der großen Erfahrung des Autors. Allerdings ist er auch knapp und anekdotisch, so daß die Anschaffung des recht teuren Buches vielleicht aus der Sicht des Kunstliebhabers lohnt, nicht aber, wenn man sich in erster Linie über bedrohte Tierarten informieren möchte.

J. Niethammer, Bonn

Radinsky, L. B.: **The Evolution of Vertrebrate Design.** Chicago, London: University Chicago Press 1987. 188 pp., £ 10.50. ISBN 0-226-70236-7

The internationally known anatomist and palaeontologist Leonhard B. Radinsky, in his last position professor of anatomy at the University of Chicago died of cancer in 1985, 48 years old. Already some time before this tragic event he had intended to write a book on the evolution of vertebrates mainly as an information source for undergraduate students. When he died the manuscript had been finished, and the work only needed further revision. This was done by Sharon B. Emerson.

In this book Radinsky tells the story of vertebrate evolution on the basis of palaeontology and comparative anatomy in an overall manner mainly discussing phylogeny on the level of classes and orders. Starting with some general remarks on fossil dating methods, principles of classification, ontogeny, comparative anatomy, and evolutionary phenomena he then continues with a characterisation of the basic vertebrate body plan and emphasizes the manifold adaptive radiations. Special bodily constructions are described in connection with functional demands of special environments and special modes of live and are valued accordingly. Drawings of skeletal and muscular elements as well as of other organs done in the way of technological constructions point out the most important evolutionary changes but also emphasize a special functional point of view. The book is well and distinctly written. It is instructive, and modern knowledge is included. There are only minor critics to be made, one of which concers the general explanations of species differences in nomenclature. Unfortunately the author chose the examples of wolf and dog not reflecting that both forms are of the same species. However, especially in this short version the book is suitable for an information on the theme.

D. Kruska, Kiel

Kulzer, E.; Valentin, H. B.; Fiedler, M.: **Fledermäuse in Baden-Württemberg.** Beih. Veröff. Naturschutz Landschaftspflege Bad.-Württ., Bd. 50, Karlsruhe 1987. 152 S.; 62 Farb- u. 19 SW-Fotos; 55 Verbreitungskarten. DM 15,–, ISBN 3-88251-122-2

Dieser Band faßt die Ergebnisse von Kartierungsmaßnahmen zusammen, die von der Arbeitsgemeinschaft „Fledermausschutz Baden-Württemberg" in den Jahren 1980–1986 durchgeführt wurden. Ziel dieser Untersuchung war es, die bekannten Fledermaus-Bestände zu erfassen, um eine Beurteilungsgrundlage für die Gefährdung der Chiropteren zu erhalten.

Nach einer kurzen Einführung in Morphologie und Ökologie der Fledermäuse werden die 20 im Untersuchungsgebiet heimischen Arten detailliert behandelt. Den zentralen Teil nehmen dabei Häufigkeit und Verbreitung der Tiere in Sommer- und Winterquartieren ein. So weit möglich, werden aber auch Angaben über die Art der Quartiere, Größe und Besonderheiten der Wochenstuben, jahreszeitliche Wanderungen und eine Schätzung der Bestandsentwicklung angeführt.

Ausführlich wird in den Schlußkapiteln auf die Gefährdung der einzelnen Arten eingegangen. Vier Spezies *(Barbastella barbastella, Miniopterus schreibersi, Rhinolophus ferrumequinum, Rhinolophus hipposideros)* müssen als ausgestorben gelten, 11 weitere sind vom Aussterben bedroht; die z. Z. noch häufigeren Arten sind ebenfalls, zumindest regional, stark gefährdet. Es wird geschätzt, daß die Gesamtpopulation in den letzten 40 Jahren um 90–95 % geschrumpft ist. Als Ursache des erschrekkenden Rückganges wird die Zerstörung von Sommerquartieren (Renovierung alter Gebäude, Fällen hohler Bäume), der Verlust vieler Winterquartiere (Zumauern von Stolleneingängen, Höhlentourismus) und die Vergiftung des Lebensraumes durch Pflanzenschutzmittel angesehen.

Dieser Band gibt nicht nur am Umweltschutz interessierten Biologen eine Fülle von Datenmaterial an die Hand, er sollte auch allen Regionalpolitikern auf den Schreibtisch gelegt werden, ohne deren verantwortungsbewußtes Handeln die Fledermäuse in unserem Land keine Zukunft haben.

U. Schmidt, Bonn

Chepko-Sade, B. D.; Tang Halpin, Z. (Eds.): **Mammalian dispersal patterns.** The effect of social structure on population genetics. Chicago–London: The University of Chicago Press 1987. 342 pp., 37 figs., 50 tables. Paperback: £ 15.95, US$ 23.95, ISBN 0-226-10268-8; hard cover: £ 43.95, US$ 65.95, ISBN 0-226-20266-1

Der Sammelband ist das Ergebnis eines 1984 in Denver, Colorado, USA veranstalteten Symposiums über Dispersionsmuster bei Säugetieren und ihren Einfluß auf die genetische Populationsstruktur. In einer Einführung definiert W. M. Shields Grundbegriffe und Ziele und erörtert Beziehungen zwischen Fortpflanzungssystem und geschlechtsgebundener Dispersion. Den Hauptteil bilden höchst interessante und gründliche Fallstudien über genealogische Beziehungen und Dispersion in Säugetierpopulationen verschiedener Arten über längere Zeiträume: Weißwedelhirsche (Nelson und Mech), verwilderte Pferde (Berger), Wölfe (Mech), Schwarzbären (Rogers), Zwergmangusten (Rood), Präriehunde (Halpin), Känguruhratten (Jones) und Pfeifhasen (Smith). In drei Studien und Referaten über Nager, vor allem *Microtus*-Arten, werden genetische Parameter einbezogen. Drei weitere Beiträge behandeln Demographie, Dispersion und genetische Struktur in menschlichen Sub-Populationen bzw. einer *Rhesus*-Kolonie. Den Abschluß bilden mathematische Modelle zu Teilfragen und eine Diskussion, in der versucht wird, aus den empirischen Daten eine effektive Populationsgröße zu berechnen, in der der Einfluß von Dispersion und Sozialverhalten berücksichtigt wird, um den Anteil sich nach Zufallsgesetzen an der Fortpflanzung beteiligender Individuen zu ermitteln und damit Populationsgrößen unter genetischen Aspekten besser vergleichen zu können.

Um einen Eindruck von der breiten experimentellen Basis der Beiträge zu geben, sei das Kapitel über *Odocoileus virginianus* angeführt: Von 1974 bis 1984 wurde die Population in einem etwa 50 km^2 großen Gebiet in Nordost-Minnesota beobachtet. 139 Tiere wurden in dieser Zeit mit Sendern markiert und z. T. mehrere Jahre lang immer wieder am Boden oder vom Flugzeug aus geortet. Daraus konnten die Beziehungen zwischen Sommer- und Wintereinständen geklärt und gezeigt werden, daß Genaustausch dort zwischen Subpopulationen, die durch unterschiedliche Wintereinstände charakterisiert sind, nur selten vorkommt.

Die Beiträge sind konzentriert und erlauben es, über ihre umfangreichen Literaturverzeichnisse die Vorgeschichte zu erschließen. Sie zeigen, daß sich keine Art wie die andere verhält, und es schwer fällt, allgemeine Gesetzmäßigkeiten abzuleiten. Die Theorie ist kompliziert und schwierig. Daher ist die sorgfältige Redaktion wohltuend, der es zu verdanken ist, daß ein innerer Zusammenhang erkennbar ist. Damit bietet der Band einen ausgezeichneten, wenn auch nicht ganz leicht lesbaren Überblick über den gegenwärtigen Forschungsstand zum Thema Dispersion, Populationsstruktur und -genetik bei Säugetieren.

J. Niethammer, Bonn

BRIEDERMANN, L.; STILL, V.: **Die Gemse des Elbsandsteingebirges.** *Rupicapra r. rupicapra.* Die Neue Brehm-Bücherei 493. 2. Aufl. Wittenberg-Lutherstadt: A. Ziemsen Verlag 1987. 122 S., 67 Abb., 20 Tab. DM 15,20. ISBN 3-7403-0041-8

Seit der Erstauflage dieses Büchleins über die von 1907 an im Elbsandsteingebirge eingeführten Gemsen sind elf Jahre vergangen. Der Gesamtbestand ist von 120 bis 130 Exemplaren im Jahr 1972 auf 200 bis 210 1984 angestiegen. Die Gliederung der Erstauflage ist beibehalten, der Inhalt jedoch um Daten aus dem letzten Jahrzehnt und Vergleichszahlen aus inzwischen erschienener Literatur vermehrt. Einige Fotos sind durch bessere ersetzt worden. Damit sind die umfassenden Beobachtungen an dieser Population forgeschritten. Für ihr Gedeihen sprechen unter anderem eine hohe Fortpflanzungsrate und eine gegenüber Alpengemsen gesteigerte Körpergröße. Auf Basalt im tschechischen Teil hat sie sich besser entwickelt als auf dem Sandstein in der DDR, vermutlich wegen der günstigeren Nahrungsgrundlage auf Basalt und der geringeren Belastung durch Touristen des Gebiets in der ČSSR. Da die geeigneten Habitate besiedelt sind, ist eine wesentliche Zunahme nicht mehr zu erwarten.

Vor allem die zahlreichen Vergleiche mit anderen Gemsenpopulationen machen dies Buch allgemein interessant und lehrreich. J. NIETHAMMER, Bonn

STERLING, K. B. (Ed.): **An International History of Mammalogy.** Vol. 1: Eastern Europe and Fennoscandia, I. Bel Air, Maryland: One World Press 1987. 198 S., 35 Abb. ISBN 0-910485-00-3.

Das vorliegende Buch ist der erste Band einer auf etwa 10 Bände angelegten Reihe, in der die Geschichte der Säugetierforschung abrißartig dargestellt werden soll. Die Idee einer „International History of Mammalogy" geht auf K. B. STERLING zurück, der sie erstmalig auf dem 1. Internationalen Säugetierkongreß in Moskau 1974 vortrug und der auch dem Werk als „General Editor" vorsteht. Ziel dieses aus forschungsgeschichtlicher Sicht zweifellos begrüßenswerten Unterfangens ist es, unter Mitarbeit von etwa 150 Fachkollegen eine Chronologie der Säugetierforschung aufzuzeichnen, wie sie sich weltweit in den verschiedenen Regionen und Ländern der Erde seit Linnaeus, 1758, darstellt. Da viele Länder nicht nur in Europa in den zurückliegenden 230 Jahren eine wechselvolle Geschichte mit vielfachen Teilungen und Grenzverlegungen zu erdulden hatten, muß eine Darstellung der nationalen Forschungsgeschichte (falls es so etwas überhaupt gibt) in den heutigen, in Europa seit 1945 festliegenden Grenzen manches Problem in sich bergen. Im jetzt vorliegenden 1. Band haben die Geschichte der Säugetierforschung für Finnland A. FORSTÉN, H. HYVÄRINEN und E. PULLIAINEN geschrieben, für Polen hat sie K. KOWALSKI aufgezeichnet. Der Beitrag über Jugoslawien stammt aus der Feder von B. DULIC. Für die Darstellung der Entwicklung in Rumänien zeichnet V. SIMIONESCU verantwortlich, während T. PESHEV die Abfassung eines Artikels über Bulgarien fertigte. Wenn auch eine gewisse Einheitlichkeit der Darstellung angestrebt war, so setzten die Autoren entsprechend der in der verschiedenen Ländern vorrangig betriebenen Forschungsrichtungen unterschiedliche Akzente. Da Forschung – auch in der Säugetierkunde – nicht anonym abläuft, sondern immer von Persönlichkeiten geprägt und vorangetrieben wird, ist Forschungsgeschichte stets mit zahlreichen Namen verbunden. Sie sind der Leitfaden, an dem sich die einzelnen Beiträge – wie auch sonst immer gegliedert – orientieren. Im Linnéschen Jahrhundert gab es eine eigenständige Säugetierforschung nirgendwo. Sie war Bestandteil zoologischer Forschung insgesamt oder ging auch in naturkundlichen Betrachtungen ganz allgemeiner Natur auf. Erst das Darwinsche Zeitalter brachte hier eine Änderung. Einen enormen Aufschwung erfuhr die Säugetierforschung in den Jahren nach dem 2. Weltkrieg, wobei länderspezifisch mal ökologisch-biologisch-populationsdynamische (Finnland, Polen), mal mehr systematisch-taxonomisch-zoogeographische Fragestellungen Vorrang hatten (Jugoslawien, Rumänien). Allen Beiträgen gemeinsam ist eine sehr begrüßenswerte Übersicht über die in den einzelnen Ländern gegenwärtig vorkommenden Arten. So erfahren wir, daß für Finnland 62 Säugetierarten, für Polen 91, für Jugoslawien 103, für Rumänien 101 und für Bulgarien 90 nachgewiesen sind. Den Artenlisten schließen sich mehr oder weniger umfangreiche, vorwiegend neuere Arbeiten berücksichtigende Bibliographien an, die aus verständlichen Gründen die Säugetierliteratur der jeweiligen Länder nur in Ausschnitten erfassen. Wer der Forschungsgeschichte aufgeschlossen gegenübersteht, sich auch rasch einmal über manchen weniger geläufigen, dennoch mit der Säugetierforschung verbundenen Namen informieren möchte, wird das Erscheinen dieses Buches und weiterer in dieser Reihe dankbar begrüßen. Am Ende des Bandes findet sich ein Index, der Personennamen, Artnamen und Sachnamen enthält. Etwas unmotiviert erscheint, daß dem Band ein Beitrag über den Säugetierschutz in Osteuropa (KIRK) angeführt ist. Dieses Thema hätte es verdient, in einem eigenen, ganz Europa berücksichtigenden Beitrag gewürdigt zu werden. H. REICHSTEIN, Kiel

Deutsche Gesellschaft für Säugetierkunde: Referate, Vorträge und Posterdemonstrationen der 62. Hauptversammlung 1988

Die Deutsche Gesellschaft für Säugetierkunde möchte mit den Kurzfassungen der Vorträge und Posterdemonstrationen der 62. Hauptversammlung eine Übersicht über die laufenden Arbeiten ihrer Mitglieder geben. Schwerpunktmäßig werden die Bereiche Ökologische Tiergeographie, Ethologie sowie Stoffwechsel und Thermoregulation behandelt. Tagungsort ist 1988 zum erstenmal Münster, obwohl die Säugetierkunde in dieser Region schon seit langem gefestigt ist. Seit Bernard Altums Arbeiten in Münster (1862) sind Gewölleuntersuchungen unverzichtbares Hilfsmittel faunistischer Forschung geworden und Hermann Landios und Emil Rade brachten 1883 die erste umfassende Regionalfauna. Mit den drei Münsterischen Institutionen Universität (Arbeiten zur Verhaltensforschung), Zoo (Zucht bedrohter Arten) und Naturkundemuseum (1984 Herausgabe einer modernen Säugetierfauna durch Schröpfer, Feldmann und Vierhaus) sind die Grundlagen für erfolgreiche Arbeiten gegeben. Kurzfassungen der Vorträge und Posterdemonstrationen der Deutschen Gesellschaft für Säugetierkunde sind ab der 58. Hauptversammlung 1984 in Göttingen noch lieferbar. Zu beziehen durch jede Buchhandlung.

★ **Deutsche Gesellschaft für Säugetierkunde, 62. Hauptversammlung in Münster, 2. bis 6. Oktober 1988.** Kurzfassungen der Vorträge und Posterdemonstrationen. Herausgegeben von Martin Berger, Münster, und Christel Schmidt, Bonn. 1988. 34 Seiten. Kartoniert 24,– DM

Verlag Paul Parey · Spitalerstraße 12 · 2000 Hamburg 1

PAUL PAREY

Erscheinungsweise und Bezugspreis 1989: 6 Hefte bilden einen Band. Jahresabonnement Inland: 318,– DM zuzüglich 13,80 DM Versandkosten, Gesamtpreis 331,80 DM einschließlich 7 % Mehrwertsteuer. Jahresabonnement Ausland: 318,– DM zuzüglich 18,– DM Versandkosten. Das Abonnement wird zum Jahresanfang berechnet und zur Zahlung fällig. Es verlängert sich stillschweigend, wenn nicht spätestens am 15. November eine Abbestellung im Verlag vorliegt. Die Zeitschrift kann bei jeder Buchhandlung oder bei der Verlagsbuchhandlung Paul Parey, Spitalerstraße 12, D-2000 Hamburg 1, bestellt werden. Die Mitglieder der „Deutschen Gesellschaft für Säugetierkunde" erhalten die Zeitschrift unberechnet im Rahmen des Mitgliedsbeitrages.

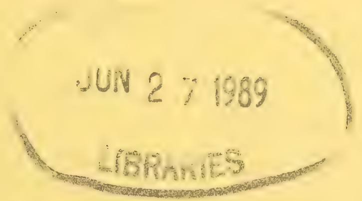
Z. Säugetierkunde 54 (1989) 1, 1–64

Vol. 54 (2), 65–128, April 1989 ISSN 0044-3468 C 21274 F



INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde



Verlag Paul Parey Hamburg und Berlin

This journal is covered by Biosciences Information Service of Biological Abstracts, and by Current Contents (Series Agriculture, Biology, and Environmental Sciences) of Institute for Scientific Information

---

Die Zeitschrift für Säugetierkunde veröffentlicht Originalarbeiten und wissenschaftliche Kurzmitteilungen aus dem Gesamtgebiet der Säugetierkunde, Besprechungen der wichtigsten internationalen Literatur sowie die Bekanntmachungen der Deutschen Gesellschaft für Säugetierkunde. Verantwortlicher Schriftleiter im Sinne des Hamburgischen Pressegesetzes ist Prof. Dr. Harald Schliemann.

Zusätzlich erscheint einmal im Jahr ein Heft mit den Abstracts der Vorträge, die auf der jeweiligen Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde gehalten werden. Sie werden als Supplement dem betreffenden Jahrgang der Zeitschrift zugeordnet. Verantwortlich für ihren Inhalt sind ausschließlich die Autoren der Abstracts.

Manuskripte: Manuskriptsendungen sind zu richten an die Schriftleitung, z. Hd. Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Biologie-Zentrum, Neue Universität, Olshausenstr. 40–60, D-2300 Kiel. Für die Publikation vorgesehene Manuskripte sollen gemäß den „Redaktionellen Richtlinien" abgefaßt werden. In ihnen finden sich weitere Hinweise zur Annahme von Manuskripten, Bedingungen für die Veröffentlichung und die Drucklegung, ferner Richtlinien für die Abfassung eines Abstracts und eine Korrekturzeichentabelle. Die Richtlinien sind auf Anfrage bei der Schriftleitung und dem Verlag erhältlich.

Sonderdrucke: Anstelle einer Unkostenvergütung erhalten die Verfasser von Originalbeiträgen und Wissenschaftlichen Kurzmitteilungen 50 unberechnete Sonderdrucke. Mehrbedarf steht gegen Berechnung zur Verfügung, jedoch muß die Bestellung spätestens mit der Rücksendung der Korrekturfahnen erfolgen.

Fortsetzung 3. Umschlagseite

© 1989 Paul Parey. Verlag: Paul Parey, Hamburg und Berlin. Anschriften: Spitalerstr. 12, D-2000 Hamburg 1; Lindenstr. 44–47, D-1000 Berlin 61. – Printed in Germany by Westholsteinische Verlagsdruckerei Boyens & Co., D-2240 Heide/Holst.

Z. Säugetierkunde 54 (1989) 65–80

ISSN 0044-3468

Grundfragen der Biokommunikation bei Säugetieren unter besonderer Berücksichtigung akustischer Signale[1]

Von G. Tembrock

Eingang des Ms. 19. 1. 1988

Abstract

Biocommunication in mammals with special references to acoustic signals

The evolution of biocommunication in mammals will be seen with respect for mesozoic reptile communicative signals. Therefore in mammals tactile, chemical and acoustic signals dominate in the first evolutional phase. The visual system was adapted to visual cues in the context of orientation and foraging behaviour. The acoustic channel of communiction has been highly specialized with respect to modulation of the frequency, an essential preadaptation for the evolution of the human communication.

Grundlagen der Biokommunikation

Biokommunikation ist definiert als „Nachrichten-Übertragung" zwischen organismischen Systemen. Wir betrachten die Biokommunikation als einen Spezialfall des Informationswechsels. Dieser wiederum ist nach unserer Auffassung eine notwendige Konstituente des Verhaltens. Anders herum: Biokommunikation ist ein Spezialfall des Verhaltens. Um sie konkret und dann auf die Säugetiere bezogen kennzeichnen zu können, sollten wir die drei Ebenen zunächst charakterisieren:

1. Ebene: Das Verhalten. Kennzeichnung: Verhalten ist organismische Interaktion mit der Umwelt auf der Grundlage eines Informationswechsels zur Optimierung der (inklusiven) Fitneß.
2. Ebene: Die Information; sie ist notwendiger Bestandteil des Informationswechsels, ein für Organismen typischer Informationsfluß. Informationen aus der Umwelt werden als „Reize" über die Exterorezeptoren perzipiert. In der Folge können sie in einer für den jeweiligen Organismus spezifischen Form einen „Sinngehalt" bekommen; er bildet auf Grund stammesgeschichtlich vorgegebener „Erkenntnis-Mechanismen" Information. Damit stellen sie eine „message" dar. Das ist nur möglich auf Grund einer Integration in den internen Zustandsraum (Motivationen, physiologischer Status usw.); Störungen in diesem Bereich würden zu einer „Fehldeutung" führen; diese Möglichkeit wird von Lebewesen als Quelle der Information auch genutzt („Tarnung", Somatolyse, Mimikry). Eine solche „Botschaft" (message) wird mit Bedeutung belegt und, bezogen auf innere und äußere Faktoren, gewichtet; sie erhält damit ein „meaning"; daraus resultiert gewöhnlich eine motorische Umsetzung in die Umwelt hinein, das äußere Verhalten. Der Informationsbegriff wird dabei im Sinne von Küppers (1986) verwendet, er ist stets nur in bezug auf einen Referenzrahmen definierbar.
3. Ebene: Kommunikation; wir sprechen von Biokommunikation, wenn es sich um biologische Kommunikationsprozesse handelt. Bei der Biokommunikation ist das unter (2) dargestellte Prinzip des Informationswechsels qualitativ dadurch verändert, daß zwischen der Konstitution der „message" und der Umsetzung in „meaning" ein externer Übertragungskanal eingeschaltet ist: Im Sender wird die Botschaft gebildet, die

[1] Vortrag gehalten auf der 61. Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde 1987 in Berlin.

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5402-0065 $ 02.50/0

für den Empfänger eine bestimmte Bedeutung (meaning) hat. Der intraorganismische Informationswechsel wurde externalisiert. Diesen Zusammenhang und die sich daraus ableitenden Parameter stellt Abb. 1 dar.

In dieser Darstellung sind verschiedene Aspekte berücksichtigt.

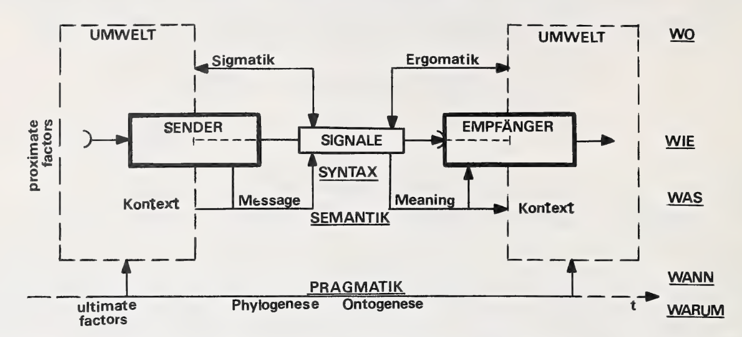


Abb. 1. Schematische Darstellung der Parameter, die im Zusammenhang mit der Biokommunikation relevant sind unter Berücksichtigung der Heuristik des Erkenntnisgewinns (Einzelheiten im Text)

Die drei Grunddimensionen der Information sind (vgl. KÜPPERS 1986):
- die *syntaktische* Dimension, die sich aus der Beziehung der Zeichen untereinander ableitet,
- die *semantische* Dimension erfaßt die Beziehung der Zeichen untereinander und das, wofür sie stehen,
- die *pragmatische* Dimension schließt beide vorgenannten ein und darüber hinaus die funktionellen Umweltbeziehungen von Sender und Empfänger.

Bei der Kommunikation sind die Zeichen „Symbole“, haben für Sender und Empfänger bereits bekannte Dimensionen; in der Verhaltensbiologie werden diese Informationsträger „Signalreize“ genannt. Damit sind sie von den „Kennreizen“ unterschieden, deren Dimensionen der Empfänger erst bestimmen muß (Informationsbildung). Die Beziehung zwischen Zeichen und Bezeichnetem erfaßt die „Sigmatik“, die Beziehung zwischen empfangenem Zeichen und Bewirktem die „Ergomatik“. So können beispielsweise Lang- oder Dehnungslaute einen stationären Status anzeigen und vielleicht auch bewirken, schnelle Lautfolgen mit Bewegung verknüpft sein. Auf diese Zusammenhänge hat besonders ZAHAVI (1982) hingewiesen. Er betont, daß Lautsignale auf Stellung und Bewegung des Signalisierenden im Augenblick der Lautäußerung hinweisen und sie daher zusätziche Information über diese Bedingungen vermitteln. Unsere Einsicht in solche Zusammenhänge ist freilich noch sehr fragmentarisch. Abb. 1 versucht auch noch eine methodische Struktur aus den untersuchten Parametern abzuleiten. Auf der Ebene der Signalübertragung ist die Frage nach dem „Wie“ relevant, durch sie werden auch die „proximate factors“ erfaßt, das unmittelbare ursächliche Geschehen, gegebenenfalls auch auf der physiologischen Ebene im Organismus. Der raumzeitliche Bezug zur Umwelt wird durch die Fragen nach dem „Wo“ und „Wann“ bestimmt, und der versierte Ethologe leitet aus den drei Fragen schließlich ein „Ethotopochronogramm“ ab. Mit dem „message“ und „meaning“ sind wir auf der semantischen Ebene, die Frage nach dem „was“ ist gestellt. Im Beispiel: Wie erfolgt die Kommunikation? Der Waldhund hebt den Hinterkörper an, stützt die Hinterfüße gegen einen Stamm und reibt die Analfläche an diesem. Was geschieht? Der Waldhund markiert sein Territorium.

Und damit bewegen wir uns auf die „letzten Fragen“ zu, bei deren Beantwortung die pragmatische Dimension gefordert ist, darüber hinaus aber auch Ontogenese und Phylogenese, denn es geht hier bei dem „Warum“ um die „ultimate factors“. Warum macht es der Waldhund gerade so und nicht anders?

Für die Kommunikation können wir nunmehr vier Voraussetzungen definieren:
1. Voraussetzung ist Kopräsenz offener Systeme,
2. Voraussetzung ist ein Informationswechsel,
3. Voraussetzung ist eine informationelle Kopplung,
4. Voraussetzung sind materiell-energetische Träger.

Der Strukturgehalt solcher Träger als „Signal“ wird „Information“ genannt. „Informationsparameter“ sind *die* Struktureigenschaften, welche diese Information enthalten.

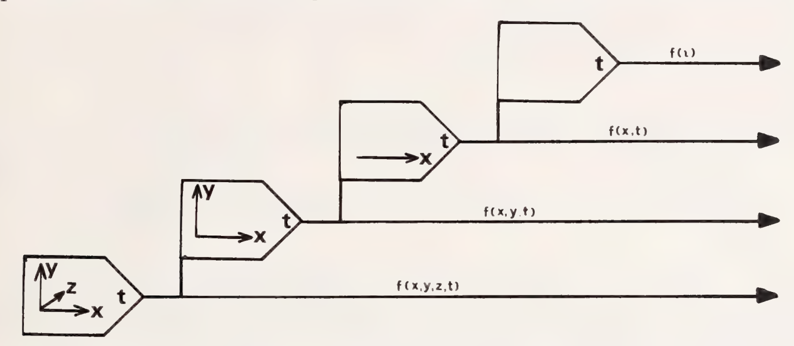


Abb. 2. Darstellung der Minimierung des Signalaufwandes in der Evolution der Signalreize

Wir gehen von der Annahme aus, daß es im Verlauf der Evolution zu einer Minimierung des Signalaufwandes gekommen ist (Abb. 2), was aber nicht ausschließt, daß aus bestimmten Gründen nebeneinander Signale verschiedenen Dimensionsgrades genutzt werden. Unsere Sprache ist der dimensionslose Extremfall. Am Anfang steht der ganze dreidimensionale Körper als Informationsträger. In der Evolution wurden die Signale vielfach vom übrigen Verhalten „abgekoppelt“, wobei die Lautgebung im Falle der aktuellen Übertragung besonders geeignet ist, während chemische Signale bei der latenten Kommunikation raumzeitlich vom Sender abgesondert und an einem Substrat deponiert werden. Wir können insgesamt drei prinzipielle Medien für die Biokommunikation unterscheiden:
- den eigenen Körper (Kontaktkommunikation),
- das Ökosystem mit seinen Strukturen,
- das Populationssystem.

Ein Verhalten, das der Übertragung von Signalen dient, bezeichnen wir als Signalverhalten (Signalhandlung). Oft ist es mit speziellen Signalstrukturen verbunden, besonders beim optischen Kanal; Demonstrationsbewegungen stellen dann Formen, Muster oder Farben zur Schau.

Ein solches Signal kann ambivalent und sowohl an den Argenossen als auch an den Predator adressiert sein, der aus ihm erfährt, daß er bereits entdeckt worden ist.

Biokommunikation wird durch die Organisationsebene der informationell gekoppelten Systeme bestimmt. Es hat bereits verschiedene Versuche gegeben, daraus eine Phylogenie der biokommunikativen Vorgänge abzuleiten, also auch die Vorstufen zu erfassen. Bekannt wurde der auch heute noch diskutable Versuch von Tavolga (1968), der folgende Ebenen unterschieden hat:
1. Die vegetative Ebene der Interaktion (physische Ebene),
2. die tonische Ebene der Interaktion mit kontinuierlichen oder auch episodenhaft ablaufenden Interaktionsprozessen,
3. die Signalebene mit echten kommunikativen Interaktionen, an denen Sender und Empfänger beteiligt sind.

Aus unserer Gesamtsicht des Verhaltens würden wir diese Ebenen wie folgt charakterisieren:

- *konnektive Ebene* mit physischer Interaktion auf stofflich-energetischer Grundlage als „substantielle Interaktion“, wie beispielsweise beim Säugen bzw. Saugen; diese Interaktion wird vor allem von den konstitutionellen Eigenschaften des Körpers bestimmt;
- *informationelle Ebene,* die durch Eigenschaften der Interaktionen mit dem Ökosystem bestimmt wird, mit der speziellen Qualität des Informationswechsels;
- *kommunikative Ebene,* bei der Sender und Empfänger durch Signalreize im Populationssystem informationell gekoppelt sind;
- *symbolische Ebene* der Interaktionen, die durch präkulturelle bzw. kulturelle Qualitäten neue Werte und Normen ausbilden;
- *sprachliche Ebene* der Interaktionen, bei der soziale und gesellschaftliche Faktoren bestimmend werden.

Die beiden letztgenannten Ebenen charakterisieren die Spezifik der Humanevolution. Diese Ebenen unterliegen einer „metabiologischen“ Selbstorganisation, die ein tradiertes Bedingungsgefüge einschließt. Alle Ebenen bilden wieder eine „Enkapsis“, jede höhere schließt die tieferen in veränderter Form mit ein, deren Gesetze weiter gültig bleiben. Wir fassen zusammen:

Verhalten: Der informationelle Zustand a (= message) bewirkt zum Zeitpunkt (t) eine Veränderung im Zustand b (= meaning); er ist intraindividuell veränderungswirksam.

Kommunikation: Der informationelle Zustand a (= message) bewirkt zum Zeitpunkt (t) in einem anderen Organismus eine Veränderung im Zustand b (= meaning); er ist interindividuell veränderungswirksam. Für die Evolution der nunmehr definierten Kommunikationsmechanismen lassen sich zwei prinzipielle Wirkungsklassen unterscheiden: Die erste möchten wir als „epiphänomenale Kommunikation“ bezeichnen. Sie ist dadurch gekennzeichnet, daß der Signalempfänger verhaltensrelevante Begleiterscheinungen des Verhaltens des „latenten Senders“ nutzt. Ein bekanntes Beispiel ist das allelomimetische Verhalten, aber dann auch die „Estampeda“ der Pferde, wobei allelomimetische Phänomene die Basis liefern. Wenn als Gruppenanpassung Synchronisation im Verhalten einen Selektionsvorteil hat, dann können „Mach-Mit-“ und Verstärker-Effekte wirksam werden, ein Phänomen, auf das kürzlich M. S. Dawkins (1986) aufmerksam gemacht hat. Solche Effekte können durch „mimische Übertreibung“ von Bewegungen noch gefördert werden. Damit ist der Weg zur zweiten großen Gruppe kommunikativer Mechanismen gebahnt, die wir als „intendierte Kommunikation“ bezeichnen möchten. Sie ist „beabsichtigt“, wobei evolutiv nochmals zwei Schritte zu differenzieren sind: 1. Der Sender vermittelt das „Meaning“, beispielsweise durch Signale, die Fluchtbereitschaft anzeigen. 2. Der Sender übermittelt die „Message“, etwa durch „Luftfeind-Warnrufe“. Wir wissen, daß bei verschiedenen Primaten sogar drei Klassen von „Feindsignalen“ möglich sind: „Luftfeind“, „Bodenfeind“ und „Feind im Geäst = Schlange“. Bei dieser höchsten Stufe der Biokommunikation wird der Empfänger durch den Sender in denselben Status versetzt, in dem sich der Sender befindet, so als hätte der Empfänger selbst die Ursache für das Signal wahrgenommen. Ein wesentlicher Aspekt verbindet sich noch mit der Frage nach den möglichen Signalwirkungen beim Empfänger. Auch hier kann eine klare Differenzierung heuristisch nützlich sein. Aus den nun bereits vorgestellten Prämissen ergibt sich folgende Struktur möglicher Signalwirkungen auf den Empfänger:

1. Änderungen in der Raumlage –
   a. Richtungsänderungen, bezogen auf das empfangene Signal (Taxis),
   b. Entfernungsänderung zur Signalquelle (Elasis).
2. Änderungen in der Zeitlage –
   a. Änderung in der Phasenlage,
   b. Änderung einer Frequenz,
   c. Änderung einer Dauer,
   d. Änderung einer Amplitude
3. Änderungen in der „Empfangsbereitschaft“ für Signale –

a. Änderung in der modalitätsspezifischen Empfindlichkeit,
b. Schwellenänderung innerhalb der Modalitäten,
c. Änderung im Bereich der Detektormechanismen, also der Ansprechbarkeit durch bestimmte Reizkonstellationen.

4. Änderungen des äußeren Verhaltens (der Motorik) –
   a. Auslösung eines bestimmten Verhaltens,
   b. Hemmung eines bestimmten Verhaltens,
   c. Modifikation eines bestimmten Verhaltens. (Diese Gruppe betrifft die typischen Auslöse-Wirkungen, im Anschluß an Wilson und Bossert 1963, auch als „releaser-effect" bezeichnet.)
5. Änderungen im internen Status (Motivation, emotionaler Status, Aktivierungsniveau, hormonaler Status, im Sinne von Wilson und Bossert 1963, auch „primer-effect" genannt).
6. Änderungen im Lernstatus –
   a. bedingte Reaktion,
   b. bedingte Aktion,
   c. komplexe Lernleistungen.

Wir wissen gegenwärtig noch wenig über die Zusammenhänge zwischen bestimmten Signalmodalitäten, -qualitäten und -quantitäten und den speziellen Wirkungsklassen, wie sie hier vorgestellt wurden. Bisher wurde immer vorrangig der Zusammenhang zur „Message" gesucht oder generell nach dem „Inhalt" der biologischen Nachrichten.

Bleibt noch ein notwendiger Hinweis auf die Modalitäten der Signale oder die möglichen „Übertragungskanäle". Die stammesgeschichtlich ältesten Übertragungswege sind der mechanische und der chemische Kanal. In beiden Fällen ist primär der Körper selbst das Übertragungsmedium. Wir bezeichnen diese Form der Signalübertragung als Kontaktkommunikation. Dieser Übertragungsweg ist bei Säugetieren bereits intrauterin gegeben, seine Bedeutung ist vielfach im Zusammenhang mit dem Verhalten unterschätzt worden, daher ist unser Wissen in diesem Kontext sehr lückenhaft. Zudem ist der Reifegrad zu berücksichtigen, den der Fetus im Uterus erreicht, insbesondere in bezug auf die Hirnentwicklung. Bei Arten, deren Hörorgane schon intrauterin funktionsfähig sind, und dazu gehört der Mensch, können akustische Signale bereits bleibende Wirkungen erzielen. Nach der Geburt sind taktil-mechanische und kontaktchemische Signale bei Säugetieren von hoher Valenz, wobei nutritive Kontakte auch chemische Signale (im Status der Konnektion, s. o.) einschließen können.

Kommunikation als motiviertes Verhalten

Unter diesen Aspekten erweist es sich als nützlich, die „Ereignisfelder motivierten Verhaltens" in die weiteren Überlegungen einzubeziehen (vgl. Tembrock 1987). Ein motiviertes Verhalten ist teleonomisch orientiert und hat daher eine Zielfunktion, beispielsweise die Kontaktaufnahme mit einem Sozialpartner. Mit dieser Verhaltensbereitschaft werden im Organismus Zielparameter (Suchbild) und funktionelle Randbedingungen sowie das entsprechende Verhaltensprogramm vorgegeben, das auch kommunikative Signale einschliessen kann. Jetzt erfolgt ein umweltbezogenes Verhalten mit Informationsaufnahme und Motorik. Stehen keine Informationen zur Verfügung, befindet sich der motivierte Organismus in bezug auf das Funktionsziel, den gesuchten Partner, noch im Distanzfeld. Das jetzt umgesetze Verhalten ist ein orientierendes Appetenzverhalten. Erst wenn Informationen über die Nähe des gesuchten Partners eintreffen, ist das Nahfeld gegeben, ein orientiertes Appetenzverhalten wird umgesetzt. Mit der Ausführung der Endhandlung ist das Kontaktfeld gegeben, auch als Terminalfeld bezeichnet (es muß nicht immer Kontakt zum Verhaltensziel bedeuten); mit der Endhandlung wird die Motivation

	KONTAKTFELD	NAHFELD	DISTANZFELD
IDENTIFIKATION Art, Geschlecht Alter Individualität	chemisch taktil	chemisch akustisch optisch	chemisch akustisch
LOKALISATION SYNCHRONISATION			
KOORDINATION Primer Effekte Releaser Effekte			

Abb. 3. Strukturmatrix zur Erfassung wichtiger Kommunikationsbedingungen bei Säugetieren. Feld 4: Schneeziege-Besprung; Feld 5: Wölfe mit koordiniertem predatorischen Verhalten; Feld 6: Zwei sich überlappende Territorien mit zeitlicher Einnischung im Überlappungsbereich; Feld 7: Kontaktverhalten bei Meerkatzen; Feld 8: Oryxantilopen im „Drohverhalten" (apotreptisches Verhalten); Feld 9: Steppenzebra beim Flehmen (nach versch. Autoren zusammengestellt)

gelöscht. In der Ontogenese und Evolution bauen sich diese Felder in umgekehrter Reihenfolge auf: Man kann nur suchen, was bekannt ist. Auch ein Kind „begreift" erst Objekte, die es dann auch aus der Entfernung identifizieren und später etwa durch Benennung erbitten kann, wenn sie nicht „präsent" (im Nahfeld) sind. Daraus leiten sich betimmte Informationsanforderungen ab, die später auch mit Hilfe der Kommunikation über andere Individuen gewährleistet werden können. Hierzu stellt Abb. 3 einige grundsätzliche Zusammenhänge vor. Im Falle der Kommunikation könnten gesuchte Partner diese Anforderungen unterstützen. Hier sei auf ein Phänomen verwiesen, das auch bei den Säugetieren einen hohen Stellenwert im sozialen Interaktionsgefüge hat und bislang kaum untersucht wurde: Die Kontaktkommunikation über mechanische Reize beispielsweise im agonistischen Verhalten, die systematisch zur Entscheidung beiträgt und ihrem Wesen nach ein „Symmetriebruch" ist: Ein Individuum dominiert. Wir übersehen gewöhnlich, daß für dieses „Kräftemessen" (wie auch beim Kontaktspiel) zahlreiche taktilmechanische Informationen genutzt werden, die Alternativen zulassen. Beim Sexualverhalten sind diese Zusammenhänge seit langem gut untersucht, aber eben nur dort.

Bei Primaten ist die herausragende Valenz dieser Informationen über den Körperkontakt (Mutter-Kind-Dyade, soziale Interaktionen) ebenfalls seit geraumer Zeit bekannt.

Evolutive Aspekte

In der Evolution der Säugetiere ergab sich in der Trias bekanntlich die Situation, daß die Reptilien alle wesentlichen für Amnioten geeigneten Lebensräume bereits okkupiert hatten. Das führte dazu, daß die Mammalia anfangs nur kleine, vermutlich dunkelaktive krallentragende (unguiculate) Arten ausbildeten, deren vorrangige Kommunikationsmittel taktile, chemische und akustische Signale waren. Der „optische Kanal" war weitgehend durch die Reptilien besetzt. Die bei den Reptilien vorbereitete Endothermie war eine Voraussetzung für diesen Evolutionsweg der Säugetiere, die zugleich die Leistungsfähigkeit des Gehirns entscheidend verbesserte, und damit wohl auch eine Basis zur Evolution des Neocortex und der Pyramidenbahnen lieferte. Der akustische Komunikationskanal hatte und hat bei Reptilien nur eine geringe Bedeutung, so daß hier eine „biokommunikatorische Nische" erschlossen werden konnte. Die chemischen Reize, die von Reptilien genutzt werden, sind fast stets Kennreize, die also informationell, aber nicht kommunikativ wirksam werden, wobei ein kontaktchemisches Verhalten unter Einsatz des Jacobsonschen Organs ein hohes Leistungsniveau ausbildete, bei einigen Schlangen noch ergänzt durch Thermorezeptoren. Doch ist weder bei ihnen noch bislang überhaupt ein gesicherter

Nachweis einer Thermokommunikation gelungen, wenigstens nicht im Bereich der „intendierten Kommunikation" (s. o.). Bei den Säugetieren gewinnt die Ausbildung des Larynx als stimmerzeugendes Organ innerhalb der Vertebraten einen singulären Stellenwert. Es wäre interessant zu prüfen, ob die phonetischen Eigenschaften dieses Stimmapparates bei der Evolution der Vögel die Herausbildung eines anders gebauten Stimmapparates gefördert haben (Syrinx).

Das Jacobsonsche Organ erfuhr bemerkenswerterweise auf Grund der zunächst exzessiven Entwicklung des Geruchssinnes („Makrosmaten") bei den Säugetieren einen Funktionswechsel und wurde wohl vollständig in den Dienst der Kommunikation gestellt; wir konnten 1964 erstmals den Zusammenhang mit dem Flehmen wahrscheinlich machen (Knappe 1964). Bei den Primaten könnte die Reduktion des Gesichtsschädels auch im Zusammenhang mit der Atrophie dieses Organs stehen. Hier wurde das taktilchemische Verhalten durch das taktilmechanische ersetzt. Mit der Rückbildung der Schuppen und der Dominanz des Haarkleides erfolgte zugleich eine einzigartige Ausbildung von Hautdrüsen im Dienst der chemischen Kommunikation, die wiederum eine „kommunikative Nische" erschloß, die bei den Reptilien fast ungenutzt blieb.

Die Ausbildung des sekundären Kiefergelenkes führte zu einer Umstellung des schallleitenden Apparates im Mittelohr auf drei Gehörknöchelchen. Der akustische Rezeptor zeigt eine Koevolution – oder besser: Koadaptation – mit den stimmerzeugenden Organen und zu deren Produkten, den Lauten. Der optische Kanal hat bei Säugetieren schon frühzeitig eine starke Ausgestaltung erfahren, anfangs im Dienst der Orientierung im Raum unter eingeschränkten Lichtverhältnissen mit Restlichtnutzung und Dominanz des Stäbchenapparates in der Netzhaut. Reduktionen scheinen abgeleitet zu sein, worauf auch jüngste Untersuchungen an Spitzmäusen *(Crocidura, Sorex)* verweisen (Sigmund et al. 1987). Gleichwohl dürfte erst im Tertiär der optische Kanal in stärkerem Umfang in den Dienst der Kommunikation gestellt worden sein, nachdem die Reptilien im Verlauf der Kreidezeit ihre dominierende Stellung verloren hatten.

Chemische Kommunikation

Die chemische Kommunikation ist vor allem in vier Funktionskreise integriert: die sexuelle Partnerbeziehung, die Alterspartnerbeziehung (Brutpflege), die biosoziale Partnerbeziehung und das Territorialverhalten, zwischen denen freilich vielschichtige Wechselbeziehungen bestehen. Eine Grundfunktion der kommunikativen Mechanismen ist mit der Distanzregulation gegeben, bei der wir drei elementare Formen unterscheiden:

- *affiner Status:* die kommunikativen Signale dienen der Distanzverringerung zwischen den Interaktionspartnern;
- *diffuger Status:* die kommunikativen Signale dienen der Distanzvergrößerung zwischen den Interaktionspartnern;
- *ambivalenter Status,* der beide vorgenannten Komponenten enthält: die kommunikativen Signale dienen der Distanzerhaltung zwischen den Interaktionspartnern.

Bei der sexuellen Partnerinteraktion haben sich zwei Typen herausdifferenziert, die mit unterschiedlichen Vorzeichen arbeiten: die affine Kommunikation im heterosexuellen Bezug und die diffuge Kommunikation im Rivalen-Bezug (gleichgeschlechtlich). Die sexuelle Kompetition hat in der modernen ethökologischen Forschung und der Gewichtung als evolutionswirksames Prinzip einen hohen Stellenwert. In der Chemokommunikation sind in den beiden letzten Jahren verschiedene Signalmechnismen bekannt geworden, bei denen Pheromone (im weiteren Sinne) distanzregulativ wirksam werden, dies auch in Hinblick auf die räumliche Verteilung von Individuen in Populationen (z. B. Jannett 1984; Cox 1984; Gosling 1985; Ryon et al. 1986).

Generell gilt für die Chemokommunikation, daß der Einsatz bestimmter Signale, die

aus spezifischen Drüsen abgesondert werden, mit einem speziellen arttypischen Verhaltensmuster verbunden ist. Die Hautdrüsen lassen sich fast ausnahmslos von zwei Grundtypen – Talgdrüsen und Schweißdrüsen – ableiten (Quay 1977). Bei vielen Arten enthält auch der Fäces chemische Signale (z. B. MacDonald 1980). *Canis aureus* markiert auf diese Weise die Grenzen eines Streifgebietes, während *Lutra lutra* diese Marken gewöhnlich im Zentrum absetzt. Auch Harn hat vielfältige Funktionen in der Chemokommunikation, wobei auch Steroid-Metabolite genutzt werden. Beim Eber enthält der Speichel Steroide (Androstenol, Androstenon), die bei den weiblichen Tieren die Immobilisationsstellung auslösen (vgl. auch Vandenbergh 1983). Auch vaginale Sekretionen können kommunikative Funktionen haben, wie es beispielsweise bei einigen Primaten nachgewiesen wurde. Beim Fremdputzen (Allogrooming) können Absonderungen von Schweißdrüsen aufgenommen werden und ebenfalls Signalwirkung haben (*Microtus agrestis*, Wilson 1973; ähnliche Befunde liegen für *M. montanus* vor, Jannett 1977). Wir finden also ein breites Spektrum solcher „semiochemischer Ladungen" bei Sekreten verschiedenster Herkunft. Dabei kann ein komplexer Zusammenhang zu verschiedensten Umweltfaktoren nachgewiesen werden. So wird die „chemische Attraktivität" bei Meerschweinchen durch die Art der Nahrung beeinflußt (Beauchamp 1976); auch bei *Acomys cahirinus* wird das Bindungs- und Wahlverhalten der Jungen von der maternalen Nahrungszusammensetzung beeinflußt (Porter und Doane 1977). Es gibt bei den chemischen Signalen saisonale Änderungen in bezug auf ihre Zusammensetzung (z. B. Adams 1980), wobei besonders gonadale Steroide Einfluß nehmen, aber natürlich auch wieder das Nahrungsspektrum wirksam werden kann. Im allgemeinen weisen die Männchen eine größere Vielfalt und höhere Intensität in bezug auf das chemokommunikative Verhalten auf als Weibchen.

Eine nicht zu unterschätzende, aber erst in einigen Fällen genauer untersuchte Bedeutung haben Lernvorgänge bei der Chemokommunikation. Dabei handelt es sich vielfach um ein obligatorisches (prägungsähnliches) Lernen, das für den Vollzug arttypischen Verhaltens notwendig ist. Der soziale Status (z. B. der Dominanzwert) kann über Chemosignale angezeigt werden; beim Biber und anderen Arten nimmt die Populationsdichte auch Einfluß auf das Markierungsverhalten (Müller-Schwarze und Heckmann 1980). Ausführliche Untersuchungen zu diesen Zusammenhängen liegen für *Tupaia belangeri* vor (von Holst 1982).

Zu bedenken ist schließlich, daß chemische Signale vielfach den Charakter einer konstitutionellen Eigenschaft haben, zur Artausstattung gehören als „konstitutionelle Signale", was ja auch für einen erheblichen Teil der optischen Signale gilt. Sie sind dann permanent (phylogenetisch) intendiert, gehen also nicht aus einer aktuellen Motivation hervor (vgl. Gesamtübersicht bei R. E. Brown und MacDonald 1985). Eine wesentliche Funktion der Chemokommunikation liegt in der Individualerkennung. Außerdem kann auf diesem Wege auch der Verwandtschaftsgrad identifiziert werden, eine Voraussetzung für die kin-selection. In jüngerer Zeit sind – ähnlich wie bei der akustischen Kommunikation – Phänomene der interindividuellen Interaktion bei der Signalabgabe bekannt geworden, die als *scent-matching* bezeichnet werden und für die Partnerwahl bedeutsam sind.

Insgesamt zeichnen sich zwei Funktionsgruppen für die chemischen Signale ab:
- Identifikationssignale: Artstatus, Geschlecht, Alter, Individuum, sozialer Status, Gruppenzugehörigkeit;
- Interaktionssignale, die auf Motivationen, Emotionen, Aktivität oder Lernen und ähnliche Verhaltensprozesse, raumzeitliche Ordnung eingeschlossen, Einfluß nehmen.

Akustische Kommunikation

Neben der chemischen Kommunikation hat bei den Säugetieren die akustische Kommunikation einen hohen Spezialisierungsgrad erreicht, der beispielsweise in bezug auf den

spektralen Bereich die Vögel weit übertrifft, deren obere Hörgrenze gegenwärtig mit 16 kHz angegeben wird. Bei Säugetieren ist eine Koadaptation zwischen Lautproduktion und Hören zu verzeichnen, die im ganzen gesehen über 100 kHz reicht. Die Lauterzeugung läßt sich wie folgt gliedern:

1. Lautproduktion 1. Ordnung (ausschließlich mit körpereigenen Mitteln) –
   a. Physiologisch determiniert, Stimmlaute mittels des Larynx sowie eines „Ansatzrohres" im Rachenbereich oder verstärkt bzw. modifiziert durch zusätzliche aerodynamische Sonderbildungen (Resonanzräume, z. B. *Symphalangus, Pongo,* einige *Cercopithecus, Odobenus*), Sonderbildungen bei Cetaceen und bei manchen Gazellen.
   b. Durch Verhalten realisiert, Friktionsgeräusche mittels Stacheln *(Hystric, Centetes)* oder Zähnen (*Wallabia,* Rodentia, Primaten, Suidae u. a.) oder Perkussionsgeräusche, Aufschlagen der Hände auf den eigenen Körper (z. B. *Gorilla, Pan*).
2. Lautproduktion 2. Ordnung mit Nutzung von Umgebungsstrukturen Bein- und Fußaufschlagen auf ein Substrat (Rodentia, Lagomorpha, Artiodactyla, aber auch Primaten).
3. Lautproduktion 3. Ordnung mit „Nutzung" von Artgenossen, „biosoziale Lautgebung" als „Supraphonation" –
   a. Duo, z. B. *Hylobates, Symphalangus,*
   b. Chor, z. B. *Canis, Panthera leo.*

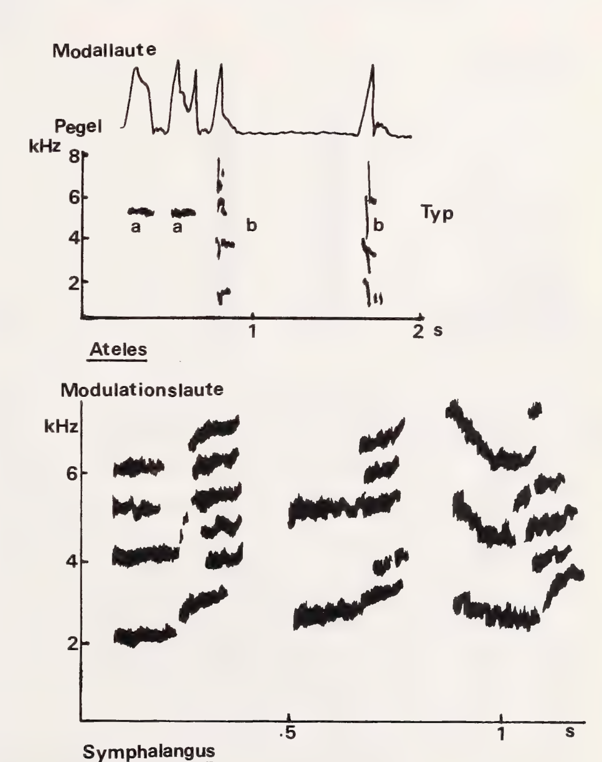


Abb. 4. Modallaute (oben) und Modulationslaute (unten) bei Primaten

Bei den Lautformen lassen sich prinzipiell Modallaute, deren Grundstruktur relativ invariant ist, von Modulationslauten unterscheiden, die durch Abwandlung variiert werden. Abb. 4 zeigt Beispiele hierfür. Bei Modallauten lassen sich daher, wie für die *Ateles*-Lautäußerungen ersichtlich, klare Lauttypen unterscheiden, die vielfach auch diskreten Situationen und inneren Zuständen zugeordnet werden können, was bei Modulationslauten nicht möglich ist; hier korrelieren Änderungen eher mit Intensitätsdifferenzen. Bei Schimpansen sind bestimmte Lautformen im hohen Maße modulationsfähig, was für den Beobachter mit dem Zustand der „Erregung" in Zusammenhang gebracht wird, also einen emotionalen Status reflektiert. Bei der Modulation ändern sich vor allem zwei Parameter:

– die Periodenfrequenz (Frequenzabstand zwischen Oberschwingungen, vgl. Abb. 5),
– die Modulationsfrequenz innerhalb des Lautes (Abb. 6).

Laute können auch die oben bereits genannten Grundstatusformen der kommunikativen Interaktion anzeigen, wobei das bekannte Gesetz der Antithese, das Darwin für optische Signale ableitete, voll realisiert wird, wie Abb. 5 für *Theropithecus* zeigt.

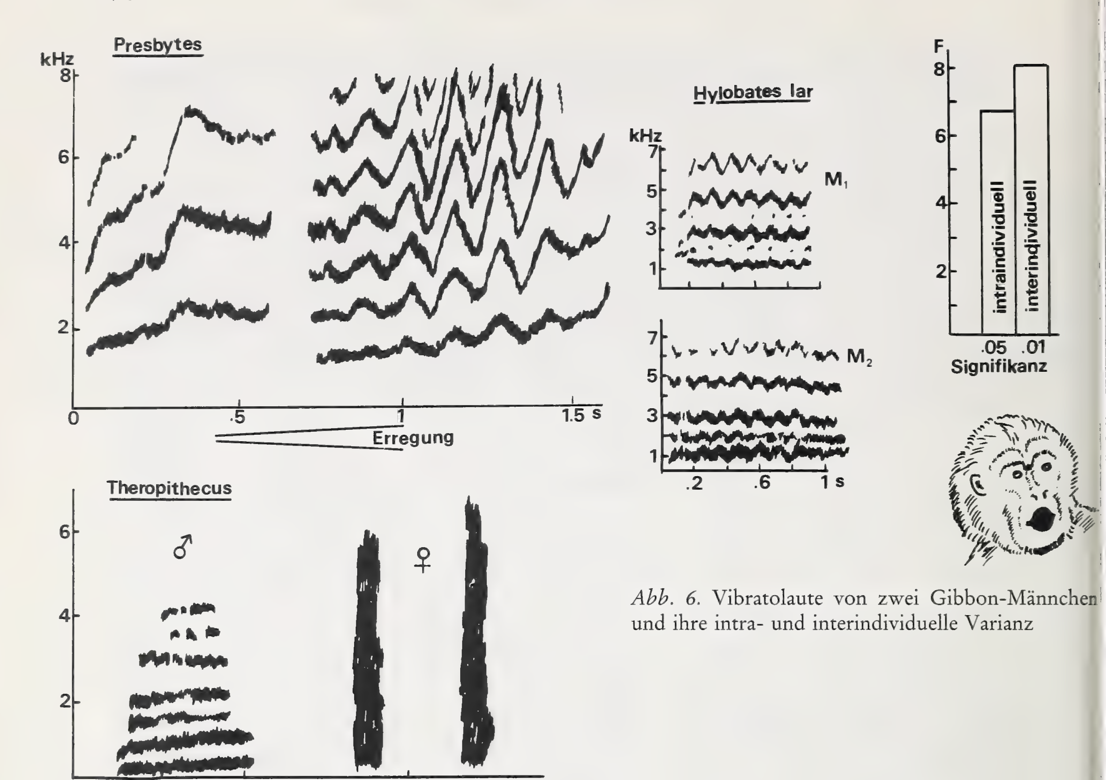


Abb. 6. Vibratolaute von zwei Gibbon-Männchen und ihre intra- und interindividuelle Varianz

Abb. 5. Änderung der Anzahl der Oberschwingungen (Periodenfrequenz) auf Grund des emotionalen Status (oben) und affiner bzw. diffuger Lauttyp (unten)

Dominanz kann aber auch durch Frequenzunterschiede angezeigt werden; bei *Rattus* hat offenbar das dominante Tier eine deutlich höhere Lautfrequenz im Ultraschallbereich (Abb. 7); ähnliches haben Gyger und Schenk (1983) bei *Apodemus* beobachtet. Wie bei der Chemokommunikation gilt auch für die akustische Kommunikation die Unterscheidung der beiden Grundfunktionsklassen, 1. Identifikationssignale und 2. Interaktionssignale. Bei der zweiten Gruppe könnten Ortungssignale eine eigene Valenz haben; bei ihnen sollten auch akustische (physikalische) Eigenschaften nachweisbar sein, die eine Lokalisation der Schallquelle erleichtern.

Die vorgelegten Beispiele weisen darauf hin, daß akustische Signale den biosozialen Status in einer sozialen Hierarchie anzeigen können. Das verbindet sich gewöhnlich mit individuellen Unterschieden. Die gegenwärtigen ethökologisch orientierten evolutionsbiologischen Fragestellungen messen dem individuellen Status einen hohen Stellenwert zu. So hat sich in jüngster Zeit die experimentelle Verhaltensbiologie verstärkt auch der Frage der Kriterien der Individualität zugewandt. Die Hypothese ist gut begründet, daß die Bedeutung von Verhaltenseigenschaften auch am Grad der kommunikativen Expression gemessen werden kann. Wenn in kommunikativen Signalen signifikant individuelle Züge manifest sind, dann sollte dies auf eine besondere Valenz dieser Individualdifferenzen hinweisen. Abb. 6 hat bereits ein solches Beispiel vorgestellt. Die beiden Männchen des Weißhandgibbons *(Hylobates lar)* zeigen in ihren Tremololauten nicht nur eine intraindividuelle Variabilität, sie unterscheiden sich auch signifikant untereinander. Das gilt in noch

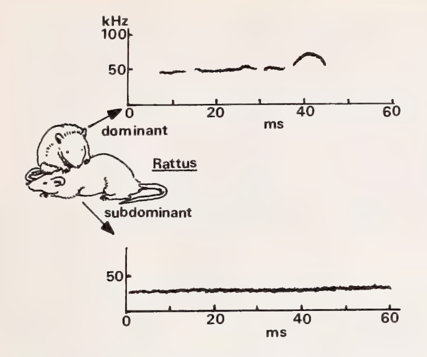


Abb. 7a. Unterschiedliche Lautformen im Ultraschallbereich bei Ratten in Abhängigkeit vom biosozialen Status (nach SALES und PYE 1974)

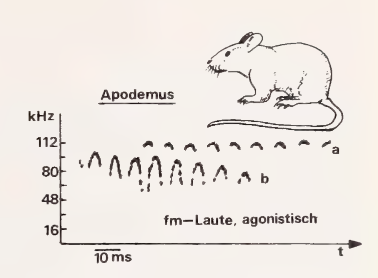


Abb. 7b. Frequenzmodulierte Laute bei Waldmäusen im agonistischen Kontext (nach GYGER und SCHENK 1983)

wesentlich höherem Maße für die Duette: Auch für das menschliche Ohr sind die typischen Paar-Duos bei den verschiedenen Gibbon-Arten unverwechselbar verschieden, wobei die Paare ihre spezielle Duo-Form langfristig beibehalten. Man wird vom Siamang beispielsweise wenigstens 15 bis 20 Paare untersuchen müssen, ehe man die arttypischen Invarianten in der Ausformung von Paar-Duos von den individualtypischen Mustern trennen kann. Auch die langen Rufreihen der Löwen zeigen individualtypische Eigenschaften, die hier vor allem die Zeitstruktur betreffen, wie unsere Untersuchungen an *Panthera leo persica* im Tierpark Berlin gezeigt haben (Abb. 8). Dabei ist erstens die Zeitstruktur der Hauptrufe in bezug auf die Periodendauer (von Lautbeginn zu Lautbeginn gemessen, vgl. auch TEMBROCK 1977a, b) deutlich verschieden und fast invariant, zweitens zeigen die Nachstoßer ein typisches Zeitmuster.

Dieses ist in so hohem Grade individualtypisch, daß die Grundstruktur auch dann erhalten bleibt, wenn die Rufreihe verkürzt wird. Diese Individualparameter werden mit Sicherheit kommunikativ genutzt, obwohl unser Wissen hierzu bei den verschiedenen Säugetiergruppen noch recht lückenhaft ist. Eindeutig funktionell ist es bei sexuellen und Alters-Partnerbeziehungen. So fanden KAPLAN et al. (1978) bei *Saimiri sciureus* sichere

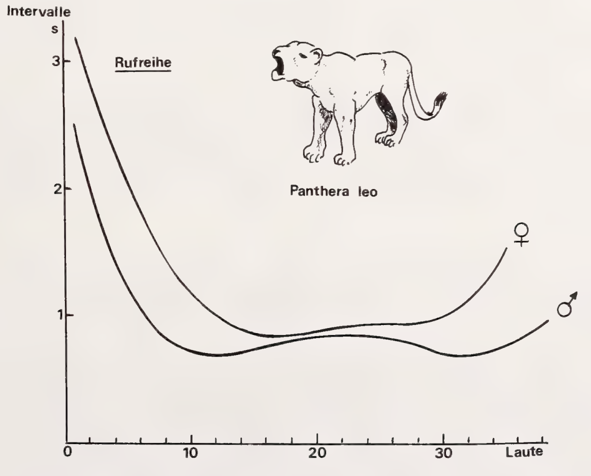


Abb. 8. Polynom 4. Grades für die Intervalle (von Lautbeginn zu Folgelautbeginn) für Mittelwerte von Rufreihen (insgesamt 14) von zwei Exemplaren des Indischen Löwen (Tierpark Berlin)

Hinweise darauf, daß Mütter ihre eigenen Jungen allein am Laut erkennen, was vermutlich für viele Primaten, den Menschen eingeschlossen (hier bei Neonaten), gilt. Wir fanden bei *Macaca,* daß 40 % aller Lautformen als Dialoge vollzogen wurden, davon 80 % als Dialoge 1. Ordnung (A–B–A); 15 % als Dialoge 2. Ordnung (A–B–A–B); 4 % als Dialoge 3. Ordnung (A–B–A–B–A); 1 % als Dialoge 4. Ordnung (A–B–A–B–A–B) (Klotz 1973).

Es gibt gegenwärtig noch wenig systematische Studien zu diesem Sachverhalt. Zur Evolution der Kommunikation gehört die Einengung des Adressaten-Spektrums:

1. Stufe: Adressat unspezifisch; Signale dieses Typs können über die Artgrenze hinaus wirksam sein;
2. Stufe: Adressat artspezifisch; die Signale sind nur an Artgenossen adressiert;
3. Stufe: Adressat intraspezifisch; die Signale sind an bestimmte Artgenossen adressiert, eine „Kaste" betreffend, z. B. Weibchen, Infantile usw.;
4. Stufe: Adressat individualspezifisch; ein bestimmtes Individuum ist der vorgesehene Empfänger;
5. Stufe: Adressat und Sender sind identisch („autospezifisch"); dies stellt einen Sonderfall des vorgenannten dar und ist typisch für die Echo-Ortung.

Eine zweite Differenzierung, die sich mit der vorstehenden im Sinne einer Matrix verbinden läßt, betrifft den Grad der Interaktion:

- Unidirektionale Kommunikation; die „Nachrichten-Übertragung" läuft nur in eine Richtung;
- bidirektionale Kommunikation; die Kommunikation ist wechselseitig *symmetrisch:* Sender und Empfänger tauschen die gleichen Signale aus; hierher gehört der elementare Typ der „Empfangsbestätigung" durch Wiederholung des empfangenen Signals; das wäre nach obigem Formalismus ein „Dialog 1. Ordnung"; Wiederholung als Redundanz; *asymmetrisch:* Sender und Empfänger tauschen unterschiedliche Signale aus; dies wieder einmalig oder mehrmalig (Dialoge n-ter Ordnung).

Stimmfühlungslaute können dem Typ nach eine Kommunikation aufbauen, die symmetrisch ist und Redundanz enthält. Sie gewährleistet einen bereits arbeitsbereiten Übertragungsweg für höhere Formen asymmetrischer Signalübertragung. Aus dieser Ableitung wird nochmals evident, welche Bedeutung individualtypische Unterschiede in der Signalausgestaltung aufweisen, sie ermöglichen selbst dann Asymmetrien, wenn der gleiche Signaltyp des Artrepertoires verwendet wird. Zudem wird individuelles Lernen damit positiv bewertet. Das hat im akustischen Repertoire der Vögel interessanterweise einen weit höheren Stellenwert als bei den Säugetieren. Hier hat erst der Mensch in der individualtypischen Sprachgestaltung diesem Prinzip einen neuen Entfaltungsrahmen gesetzt.

Nach allem, was wir bislang von der Kommunikation bei Primaten wissen, ist in der Gestik und Mimik der individuelle Spielraum für die Ausgestaltung ungleich größer und mit höheren Lernpotenzen ausgerüstet als im Bereich der akustischen Kommunikation. Das sollte bei Entwürfen zur Evolution der Sprache als Mittel der Kommunikation bedacht sein.

Evolutive und ontogenetische Aspekte der akustischen Kommunikation

Mit diesen Bemerkungen ist erneut die Evolution der Biokommunikation angesprochen. Doch geht es jetzt speziell um die akustischen Phänomene bei den Primaten und mit Blick auf die Humanevolution. Untersuchungen am Alarmschrei Neugeborener lassen Umrisse einiger neuer Vorstellungen hierzu erkennen, die Mende und Wermke (Wermke 1987; Mende und Wermke im Druck) formuliert haben. Ihre Gedanken seien abschließend hier kurz vorgestellt, wobei auch an dieser Stelle auf die Notwendigkeit von ontogenetischen

Studien verwiesen sein soll: Nach Ploog (1981) lassen sich in der Lautontogenese des Menschen drei Stufen unterscheiden:

1. Automatische Steuerung angeborener Lautmuster,
2. bedingter, nicht streng reizgebundener Einsatz der arteigenen Lautmuster;
3. voluntative Produktion erlernter Lautfolgen.

Ihre Ontogenese läßt sich mit der funktionellen Reifung des neuronalen Substrates verbinden. Beim menschlichen Säugling gehören zum arttypischen Repertoire die Schreie sowie die „Nicht-Schrei-Vokalisationen“ (Morath 1979) und auch die „Gurr-Laute“ nach der 6. bis 8. Lebenswoche (vgl. Lenneberg 1972). Ab 6. Monat setzt dann das „Babbeln“ („Lallen“) ein, das sich durch eine hohe Mannigfaltigkeit in bezug auf Bildungsstelle, Klangfarbe, Tonbewegungen, Rhythmus sowie Akzentuierung auszeichnet, auch Artikulationsstellungen und Bewegungsabläufe variieren erheblich (vgl. Siegert 1973). Es gibt Hinweise, daß Erwachsene mit etwa 80 % Wahrscheinlichkeit in diesem Alter Kinder der eigenen Sprachregion von Fremden unterscheiden können, was dann wieder verloren geht. Bei den „Lallmonologen“ ist die Eigenkontrolle offenbar wichtiges Element, so daß Jakobson (1969) von „Autoecholalie“ sprach. Wir sehen auch hier einen Zusammenhang zur adäquaten Reifung der funktionellen Strukturen, die eine spätere Entwicklung des Sprechens gewährleisten.

Diese lerngesteuerten, genetisch determinierten Vorgänge schaffen eine eigene Qualität des „Selbsterlebens“, sicher eine wichtige Voraussetzung für die speziellen Bewußtseinsparameter beim Menschen. Kinder mit Kiefer- oder Gaumenspalten, deren Lallphase entscheidend beeinträchtigt war, ehe eine operative Korrektur erfolgte, zeigen später erhebliche Sprachstörungen, obwohl die Sprechorgane nun funktionsfähig sind. Offensichtlich ist die „Ko-Ontogenese“ im vokal-auditiven System durch die Beeinträchtigung der Lallphase gestört. Der Organismus erzeugt in dieser Phase das akustische Reizfeld autonom und weitgehend umgebungsunabhängig, ein „total feedback“ (Fisch 1983) ist gegeben: Das auditorische Feedback macht eine Internalisation des kommunikativen Verhaltens möglich und leistet damit einen wichtigen Beitrag zur Ontogenese kognitiver Fähigkeiten. Mende und Wermke weisen auf die spezielle Systemorganisation und biophysikalisch-energetische Zusammenhänge hin. Die Energieflußdichte ist bei akustischen Signalen wesentlich niedriger als bei optischen. Im zentralen Bereich (200 lux, 60 Db) sind die Energieflußdichten von Licht millionenfach höher als die Flußdichten von Schall. Das liefert aus energieökonomischen Gründen ein wesentliches Argument für die besondere Eignung selbsterzeugter akustischer Signale gegenüber optischen.

Die Schallübertragung über das Medium Luft führte zu einer Verbesserung des Hörvermögens gegenüber den wasserbewohnenden Vorfahren der höheren Wirbeltiere, bei Säugetieren zu einer Verschiebung des Maximums der Empfindlichkeit hin zu höheren Frequenzen sowie einer Verbreiterung des Hörbereiches (Fleischer 1984). Bei den Carnivoren wurden die Empfindlichkeitsmaxima bis zu den physikalischen Grenzen ausgeweitet, wobei Habitatanpassung unter Einschluß der jeweiligen Besonderheiten in den Übertragungseigenschaften des Schalls zu differenzierten Sonderentwicklungen führte.

In diesem Zusammenhang hat das Frequenzunterscheidungsvermögen eine eigene Entwicklung vollzogen, wobei ein deutlicher Evolutionstrend auch in den rezenten Modellen der Ahnenreihe zum Menschen hin erkennbar ist (Abb. 9). Diese Diskriminationsfähigkeit stand sicher primär im Zusammenhang mit der Informationsgewinnung aus ökologischen Parametern der Umgebung, sie wurde erst später auch für die eigentliche Kommunikation genutzt. Die Coevolution hat beim Menschen zur gleichen Präzision in Lautperzeption und Lauterzeugung geführt: Die Präzision der Phonation (Jitter) stimmt mit der Präzision des Hörens (Frequenzhub frequenzmodulierter Signale) überein. Die höchste Ausformung hat diese Entwicklung beim Gesang erfahren in der Umsetzung frequenzkonstanter und frequenzmodulierter Laute. Die biokommunikative Valenz sol-

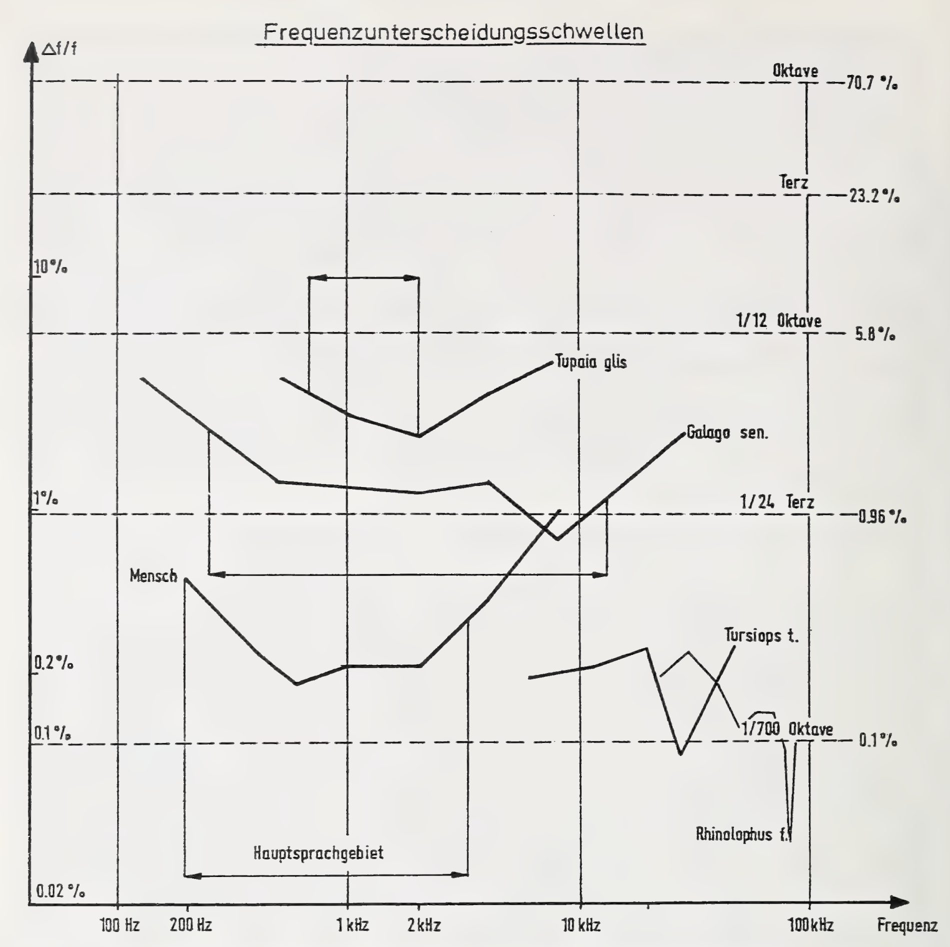


Abb. 9. Beispiele zur Darstellung der Evolution der Frequenzunterscheidungsschwellen (nach Mende und Wermke, im Druck)

cher Eigenschaften hängt auch mit dem deutlichen Signal-Rausch-Abstand in Ökosystemen zusammen, da in der Natur frequenzmodulierte Schallereignisse (> 3 Hz) selten sind. Bei den Säugetieren und speziell den Primaten ist daher die Evolution kommunikativer Signale durch verstärkte Nutzung der Frequenzmodulation gekennzeichnet. Der Bereich des besten Frequenzunterscheidungsvermögens und der Bereich der häufigsten Soziallaute fallen daher zusammen. Die reizintensive und stark „erregende" Wirkung frequenzmodulierter Signale wird auch in der modernen Zivilisation bei Alarmsignalen genutzt. Auch der Säuglingsschrei als ein Alarmsignal zeigt daher solche Eigenschaften. Daraus leiteten Mende und Wermke ein mehrjähriges Forschungsprogramm ab, in dem das spezielle Variabilitätsmaß „Melodienspektrum" entwickelt wurde. Abb. 10 zeigt zwei Beispiele hierfür: Beim gesunden Kind (erste Lebenstage) ist dieses Spektrum stark gegliedert, bei einem zerebralparetischen Kind dagegen auffallend monoton. Dieser Variabilitätsverlust bei der Grundfrequenz scheint auf unreifer oder gestörter Hirnstammfunktion zu beruhen. Die diagnostische Valenz ist unübersehbar.

Die vorstehenden Ausführungen konnten nur einige grundlegende Wesenszüge in der Biokommunikation bei Säugetieren charakterisieren, wobei das Vorgehen auch vom

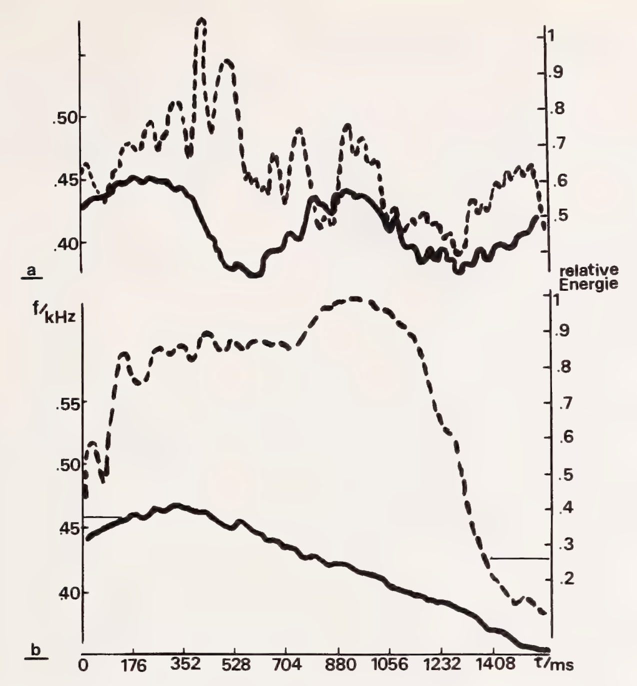


Abb. 10. a. Starkstrukturiertes Melodiespektrum eines gesunden neugeborenen Säuglings; b. Melodiespektrum eines Säuglings, der später zerebralparetisch wurde. Das Spektrum ist ungegliedert und monoton abfallend (nach Wermke 1987)

gegenwärtigen Wissensstand mitbestimmt wird. Moderne übergreifende Fragestellungen, wie sie vor allem durch die Ethökologie und die Verhaltensphysiologie angeboten werden, lassen aber bereits fruchtbare Felder neuen Erkenntnisgewinns in Umrissen sichtbar werden. Hier wurde versucht, einige durch spezifische Aspekte der gegenwärtigen Forschung erkennbare Ansätze und Quellpunkte für weiterführende Untersuchungen aufzuzeigen. Sie werden sowohl von den künftigen Konzepten der Evolutionstheorien als auch von weiteren Einsichten in die speziellen Bedingungen der Biokommunikation mitbestimmt. Nicht zuletzt sollte dabei das wachsende Bemühen um neue Einsichten in die Bedingungen der Humanevolution mit in Rechnung gestellt werden.

Zusammenfassung

Die Biokommunikation der Säugetiere hat ihre spezielle Qualität durch die Konkurrenz mit den Reptilien im Mesozoikum erhalten. Es dominierten anfangs taktile, chemische und akustische (mechanische) Signale; das Auge war zunächst vorrangig auf den Informationsgewinn aus ökologischen Parametern spezialisiert und wurde wohl erst im Tertiär stärker zur Aufnahme optischer Signale von Artgenossen genutzt, also in den Prozeß der Biokommunikation einbezogen. Der akustische Kanal hat sich hochgradig spezialisiert unter besonderer Berücksichtigung frequenzspezifischer Parameter (Frequenzmodulation) und hierin einen singulären Stand erreicht, der auch Voraussetzung für die Evolution der menschlichen Kommunikation war.

Literatur

Adams, M. G. (1980):: Odour-producing of mammals. Symp. Zool. Soc. **45**, 57–86.
Beauchamp, G. K. (1976): Diet influence attractiviness of urine in guinea pigs. Nature **263**, 587–588.
Brown, R. E.; MacDonald, D. W. (1985): Social odours in Mammals. Oxford: Oxford Univ. Press.

Cox, T. P. (1984): Ethological isolation between local populations of house mice *(Mus musculus)* based on olfaction. Anim. Behav. **32**,1068–1077.
Dawkins, M. S. (1986): Unravelling animal behaviour. Burnt Mill, Harlow: Longman.
Fisch, L. (1983): Integrated Development and Maturation of the Hearing System. Brit. J. Audiol. **17,** 137–154.
Fleischer, G. (1984): Evolution of ear and hearing in mammals. Acta Zool. Fennica **171,** 77–81.
Gosling, L. M. (1985): The even-toed ungulates: order Artiodactyla. Sources, behavioural context, and function of chemical signals. In: Social Odours of Mammals. Ed. by R. E. Brown and D. Mac Donald. Oxford: Oxford University Press, 550–618.
Gyger, M.; Schenk, S. (1983): Semiotical approach to the ultrasonic vocalization in the woodmouse, *Apodemus sylvaticus* L. Behaviour **84,** 244–257.
Holst, D. von (1985): Olfactory communication in *Tupaia belangeri:* Chemical signals – their effects and possible functions. In: Social Odours of Mammals. Ed. by R. E. Brown and D. MacDonald. Oxford: Oxford Univ. Press.
Jakobson, R. (1969): Kindersprache, Aphasie und allgemeine Lautgesetze. Uppsala Univers. Aarskrift, Neuausgabe Ed. Suhrkamp.
Jannett, F. J. (1977): On the sociobiology of the montane vole, *Microtus montanus nanus* (Rodentia: Muridae). Ph. D. Thesis, Cornell Univ., Ithaca, New York.
— (1984): Scent communication in social dynamics of mammals. Acta Zool. Fennica **171,** 43–47.
Kaplan, J. N.; Winship-Ball, A.; Sim, L. (1978): Maternal discrimination of infant vocalizations in squirrel monkeys. Primates **19,** 187–193.
Klotz, M. (1973): Zum Problem der bidirektionalen akustischen Kommunikation bei der Gattung *Macaca.* Z. Psychol. **180/181,** 283–310.
Knappe, H. (1964): Zur Funktion des Jacobsonschen Organs (Organon vomeronasale Jacobsoni). Zool. Garten N. F. **28,** 188–194.
Küppers, B.-O. (1986): Der Ursprung biologischer Information. München, Zürich: Piper.
Lenneberg, E. H. (1972): Biologische Grundlagen der Sprache. Frankfurt: Suhrkamp.
Mende, W.; Wermke, K. (im Druck): Evolution und Ontogenese der auditiv-vokalen Systems. Wiss. Zeitschr. Humboldt-Univ., Math.-Nat. Reihe, Berlin.
Morath, M. (1979): Inborn vocalizations of the human baby and communicative value for the mother. E.B.B.S. workshop „Audition and Speech“, Göttingen.
Müller-Schwarze, D.; Heckman, S. (1980): The social role of scent marking in beaver *(Castor canadensis).* J. Chem. Ecol. 6, 81–95.
Ploog, D. (1981): Neurobiology of primate audio-vocal behavior. Brain Res. Rev. **3,** 35–61.
Porter, R. G.; Doane, H. M. (1977): Diatary-dependent cross-species similarities in maternal chemical cues. Physiol. and Behav. **19,** 129–131.
Quay, W. B. (1977): Structure and function of skin glands. In: Chemical Signals in Vertebrates. Ed. by D. Müller-Schwarze and M. N. Mozell. New York: Plenum Press. 1–16.
Ryon, J.; Fentress, J. C.; Harrington, F. H.; Bragdon, S. (1986): Scent rubbing in wolves *(Canis lupus):* The effect of novelty. Can. J. Zool. **64,** 573–577.
Sales, G.; Pye, D. (1974): Ultrasonic Communication by Animals. London: Chapman and Hall.
Siegert C. (1973): Entwicklung der Sprache und des Sprechens. In: Phoniatry und Pedioaudiologie. Ed. by Biegalski et al. Stuttgart, 91–103.
Sigmund, L.; Siegmund, R.; Claussen, C.-P. (1987): Bau und Funktion der optischen Sinnesorgane bei der Waldspitzmaus *(Sorex araneus)* und der Gartenspitzmaus *(Crocidura suaveolens)* und ihre Beziehung zum lokomotorischen Verhalten. Zool. Jb. Physiol. **91,** 63–78.
Tavolga, W. N. (1968): Fishes. In: Animal Communication. Ed. by T. A. Sebeok. London: Indiana University Press, 271–288.
Tembrock, G. (1977a): Zeitmuster akustischer Signale. Nova Acta Leopoldina **46,** 581–606.
Tembrock, G. (1977b): Zeitmuster in der organismischen Kommunikation. Biol. Zbl. **96,** 641–664.
Tembrock, G. (1987): Verhaltensbiologie. Jena: VEB Gustav Fischer Verlag.
Vandenbergh, J. G. (Ed.) (1983): Pheromones and Reproduction in Mammals. New York: Academic Press.
Wermke, K. (1987): Begründung und Nachweis der Eignung des Säuglingsschreis als Indikator für zentralnervöse Funktionsstörungen des Neugeborenen – Fallstudien unter Einsatz eines speziellen Computerverfahrens. Diss. Humboldt-Univ. Berlin.
Wilson, E.-O.; Bossert, W. H. (1963): Chemical communication among animals. Recent Progress **19,** 673–716.
Wilson, S. (1973): The development of social behaviour in the vole *(Microtus agrestis).* Zool. J. Linn. Soc. Lond. **52,** 45–62.
Zahavi, A. (1982): The pattern of vocal signals and the information they convey. Behaviour **80,** 1–8.

Anschrift des Verfassers: Prof. Dr. Günter Tembrock, Bereich Verhaltenswissenschaften, Sektion Biologie, Humboldt-Universität Berlin, Invalidenstr. 43, DDR-1040 Berlin

Z. Säugetierkunde 54 (1989) 81–99

ISSN 0044-3468

Natural selection of body size differentiation in Spiny mice, *Acomys*

By E. Nevo

Institute of Evolution, University of Haifa, Mt. Carmel, Haifa 31999, Israel

Receipt of Ms. 29. 5. 1987

Abstract

Tested morphometrics of spiny mice, *Acomys*, of 181 specimens from 7 localities in Israel and Sinai, to evaluate the factors effecting body size differentiation. These specimens represent 3 karyotypes (2 formal species) comprising 5 populations of *Acomys cahirinus* (2n = 38); 2 populations of *A. cahirinus* (2n = 36); and 3 populations of *Acomys russatus* (2n = 66). Each population of the latter is sympatric with *A. cahirinus*. The 7 localities represent a general southward transect of increasing aridity. The results indicate that: 1. body characters varied significantly between localities. Body weight and length decreased, whereas tail, ear and relative forefoot and hindfoot lengths generally increased with aridity in accordance with the Bergmann rule. 2. Morphology was found to be partly correlated with allozymic variation.

The geographic patterns and climatic correlates and predictors of morphological variation in *Acomys* in Israel and Sinai indicate that natural selection, mediated by climatic and biotic factors, is a major cause of body size differentiation. The latter in turn contributes to improving thermoregulatory efficiency and optimizes the energetics balance.

Introduction

Body size is subject to differentiation by both direct and indirect multiple evolutionary factors. These involve, among others, ecological (e.g., climatic, habitat, resource availability and biotic interactions), physiological (e.g., metabolism, food resources and energetics), demographic (e.g., population size, intra- and interspecific competition) and pathogenicity (e.g., parasites and diseases) factors. Their relative importance and complex interaction vary spatiotemporally, hence must be evaluated specifically in each case. For a general discussion of the functional significance of variation in body size among mammals, see Clutton-Brock and Harvey (1983). For a discussion of the general variation and correlates of body size in mammals, see Eisenberg (1981). Since heritability of body size in mammals is usually high (Shields 1962), geographic variation in size differentiation must involve a relatively high genetic component subject to natural selection. The objective of this study was to investigate the body size differentiation in spiny mice, genus *Acomys*, in Israel, and hypothesize about its possible determinants.

Spiny mice, genus *Acomys*, are tropical murid rodents (Rodentia, Myomorpha, Murinae) involving about 18 species ranging in Africa and southwest Asia in rocky habitats. Two species of spiny mice, the common spiny mouse, *Acomys cahirinus*, and the golden spiny mouse, *Acomys russatus*, occur in Israel and Sinai (Shkolnik and Borut 1969; Haim and Borut 1974, 1975). *A. cahirinus* is widely distributed in Israel and Sinai (Fig. 1), ranging in both mesic and xeric environments comprising the Mediterranean, steppe and desert climatic regimes and is thus a climatically euryoek species in range (Table 1). However, it lives only in rocky areas, and is therefore relatively stenotopic, or narrow in niche structure. Two chromosome forms of *A. cahirinus*, which differ by a single Robertsonian change, occur in Israel and Sinai (Wahrman and Goitein 1972, and Fig. 1). The Israeli populations possess 2n = 38 chromosomes, and those from Sinai have 2n = 36

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5402-0081 $ 02.50/0

chromosomes. The two chromosome forms are completely homozygous except for a hybrid zone, about 16 km long and 15 km wide, where 2n = 37 hybrids were also found. The two chromosome forms are morphologically indistinguishable, but have not as yet reached complete reproductive isolation. Although designated as the northern or "Israeli Form" and southern or "Sinaitic Form" (WAHRMAN and GOITEIN 1972) they may be viewed, owing to their chromosomal homozygosity across vast ranges, as derivatives of a relatively recent event of speciation, displaying currently its final stages (NEVO 1985). The fossil record indicates that *A. cahirinus* is an upper Palaeolithic colonizer in humid Mediterranean Israel, i.e., it presumably appeared some 20.000–30.000 years ago (TCHERNOV 1968). Therefore, its morphological differentiation in Israel is relatively recent and traceable over time.

A. russatus is similar in morphology and life history to the *A. cahirinus* complex, but it differs from the latter in karyotype (2n = 66, WAHRMAN and ZAHAVI 1953); in its restricted distribution in extreme desert habitats (either hot or cold), in its narrower niche, and in its unique physiological adaptations (SHKOLNIK and BORUT 1969; HAIM and BORUT 1974, 1975, 1981). It occurs sympatrically with *A. cahirinus* (either 2n = 38 or 2n = 36) and shares the same rocky habitat. However, while *A. cahirinus* is nocturnal, *A. russatus* is frequently diurnal (SHKOLNIK 1971). The genetic differentiation and speciation of spiny mice in Israel have been recently studied (NEVO 1985) and will be related to the morphometric differentiation in the discussion. Here I present evidence suggesting that body size differentiation in *Acomys* relates primarily to climatic and biotic determinants.

Material and methods

Sampling

A total of 181 (113 males and 68 females) specimens from 7 localities representing 10 populations and 3 karyotypes were sampled in Israel and in Sinai. These involved 5 (1–5) populations of *A. cahirinus* (2n = 38); 2 populations (6, 7) of *A. cahirinus* (2n = 36), and 3 populations (8–10) of *A. russatus*, each population being sympatric with a counterpart of *A. cahirinus* (8 with 4, 9 with 6 and 10 with 7). Data on localities and ecogeographical parameters are given in Table 1; distribution and sampling localities are shown in Fig. 1. Sampling was conducted in the autumns of 1975 (in Israel) and 1976 (in Sinai) and each sample was collected in an area of about one km^2. The seven localities of the samples are distributed largely along a transect of increasing aridity (see Table 1 and Fig. 1).

Morphological measurements

To demonstrate the range of phenotypic variation in the 3 karyotypes of *Acomys*, 6 measures were taken of each adult mouse (and averaged separately for each sex): body weight, and lengths of body, tail, forefoot, hindfoot and ear. The ratios of the last four measures to body length were calculated.

Statistical analysis

Stepwise multiple regression (SPSS-x 1986) was used to determine whether phenotypic variation of morphological traits is influenced by and associated with environmental factors. In addition, Pearsonian correlations were computed between all variables including allozymic (see NEVO 1985) and morphological variation. The variance in morphology within and between populations was tested by analysis of variance, ANOVA.

Results

Patterns of morphometric variation

The means of morphometrics of body characters for the 10 populations examined are given for males and females separately (Tables 2a and 2b), and the regressions of body weight and relative tail and ear sizes on latitude, temperature and the aridity index as expressed by

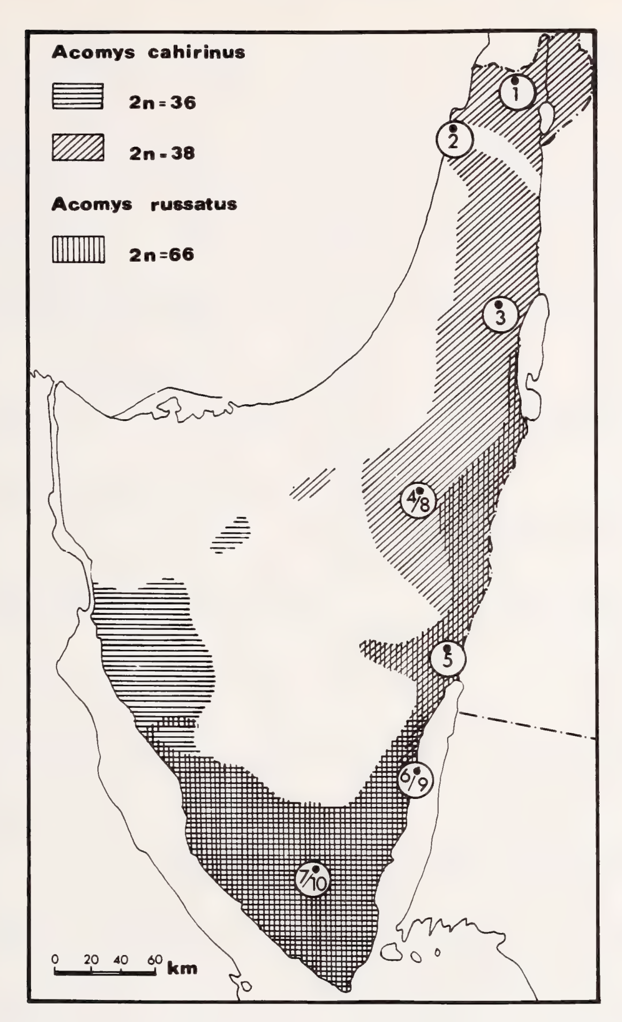


Fig. 1. The distribution of the three karyotypes of *Acomys,* and the sampled populations: *A. cahirinus* (2n = 38): 1 = Hurfeish; 2 = Beit Oren; 3 = Jerusalem; 4 = Mitzpe Ramon; 5 = Timna. *A. cahirinus* (2n = 36): 6 = Neviot; 7 = Santa Katharina. *A. russatus:* 8 = Mitzpe Ramon; 9 = Neviot; 10 = Santa Katharina

rainfall are given in Figure 2 in several scatter diagrams. A statistically significant amount of variation between localities (in most cases of *A. cahirinus,* $p < 0.001$) was found for all body characters and ratios (Tables 2a and 2b). The following trends were found in *A. cahirinus* (note that males are better sampled than females). In general, body weight and length decreased southward (Fig. 2), whereas the lengths of tail, feet, ear and the ratios of all extremities of body length largely increased southward, along with an increase in aridity and temperature (Fig. 2). Body weight in *A. cahirinus* decreases from Hurfeish to Santa Katharina by 17.5 % and 19.7 % for males and females, respectively.

In *A. russatus,* which is represented by only 3 localities, the following trends were found. Body weight and length decreased in both sexes southward from the cool Negev highlands of Mitzpe Ramon to the hot Sinai lowlands of Neviot. Body weight decreased 32.7 % and 27.6 % for males and females, respectively. By contrast, a reverse trend is

Table 1. **Geographical and climatological data for 7 localities in Israel and Sinai in which 3 karyotypes, *Acomys cahirinus*[2] and *Acomys russatus* and 10 populations of *Acomys* were sampled[1]**

Species	Pop. No.	Locality	Sample size (N)	Longitude (Ln) (decimal)	Latitude (Lt) (decimal)	Altitude (Al) (m)	Mean Temperature (°C) Annual (Tm)	Mean Temperature (°C) Jan. (Tj)	Mean Temperature (°C) Aug. (Ta)	Annual rainfall (Rn) (mm)	Humidity at 14:00 (Hu) (%)	Annual evaporation (EV) (cm)
A. cahirinus	1	Hurfeish	19	35.40	33.03	800	18.0	8.0	26.0	750	40.0	192
A. cahirinus	2	Bet Oren	22	35.00	32.73	425	20.5	11.0	26.0	688	58.8	190
A. cahirinus	3	Jerusalem	17	35.23	31.78	700	18.5	10.0	25.0	486	54.0	220
A. cahirinus *A. russatus*	4 8	Mitzpe Ramon	26 11	34.80	30.60	860	19.4	12.0	25.0	78	38.7	240
A. cahirinus	5	Timna	14	35.03	29.88	80	25.0	14.0	36.0	32	27.0	360
A. cahirinus *A. russatus*	6 9	Neviot	22 23	34.60	29.05	30	26.0	16.0	37.0	20	25.0	380
A. cahirinus *A. russatus*	7 10	Santa Katharina	13 14	33.92	28.58	2200	10.8	1.0	18.0	64	26.0	320

[1] Climatic data are multiple year averages reported by the Israel Meteorological Service. – [2] The *A. cahirinus* complex involves 2 chromosomal karyotypes.

apparent in body weight which increases again toward the cold mountain tops of southern Sinai in Santa Katherina. Body weight increased 33.1 % and 27.8 % in males and females, respectively.

An opposite trend was displayed by the relative tail and foot sizes of this species. In the better sampled males, they increased from Mitzpe Ramon to hot Neviot, but decreased again in cold Santa Katharina (see trends in Table 2). These reverse trends from Neviot to Santa Katharina are inconsistent in *A. cahirinus.*

Environmental correlates and predictors of morphological variation

Pearsonian correlations

In the search for environmental correlates of morphological variation we used several geographic and climatic variables (Table 1): Longitude = Ln; Latitude = Lt; and Altitude = Al, were used as geographic variables. Temperature (mean annual = Tm; mean January = Tj; and mean August = Ta) and moisture (mean annual rainfall = Rn; mean midday relative humidity = Hu; and mean annual evaporation = Ev) were used as climatic variables. To assess the ecological background structure the correlation matrix of the ecological variables was analysed. Following are some correlations, where

Table 2a. **Morphometrics of adult *Acomys cahirinus* and *Acomys russatus* accompanied by analysis of variance (ANOVA); Males**

Species	2n	Pop No.	Locality	Sample size N	Weight (g) Mean	Weight (g) S.D.	Body Mean	Body S.D.	Tail[a] Mean	Tail[a] S.D.	Forefoot Mean	Forefoot S.D.	Hindfoot Mean	Hindfoot S.D.	Ear Mean	Ear S.D.
							Length (mm)									
A. cahirinus	38	1	Hurfeish	12	45.12	9.1	106.3	7.4	98.8	6.1	9.08	0.7	18.58	0.7	12.50	0.9
		2	Bet Oren	11	44.66	6.8	117.1	5.6	98.2	9.0	9.56	0.9	19.00	0.5	11.78	0.8
		3	Jerusalem	11	39.65	4.8	108.5	7.0	97.3	8.2	8.64	0.9	18.27	0.5	13.00	0.9
		4	Mitzpe Ramon	11	50.03	11.9	112.0	7.2	106.3	6.6	9.09	0.7	17.64	2.4	16.00	2.6
		5	Timna	12	38.27	8.1	100.8	9.9	109.9	6.4	9.58	1.0	18.92	1.4	14.08	0.9
	36	6	Neviot	15	36.35	4.6	102.2	8.0	111.8	5.0	9.60	1.2	18.73	1.0	15.07	1.1
		7	Santa Katharina	8	37.24	8.2	105.5	6.7	105.8	7.3	9.13	1.4	19.50	0.8	15.75	1.0
			Total	80	41.58	8.9	106.9	9.0	104.2	8.6	9.26	0.90	18.63	1.3	14.07	1.9
			F[b]		4.67***		5.87***		5.55***		1.81 n.s.		2.28*		15.96***	
A. russatus	66	8	Mitzpe Ramon	7	63.31	7.1	112.4	3.6	72.3	5.3	9.14	0.9	18.00	1.0	11.43	2.0
		9	Neviot	15	42.61	9.4	105.3	7.0	69.6	6.7	9.47	1.1	18.53	1.1	10.53	1.1
		10	Santa Katharina	11	56.72	17.9	114.7	6.9	61.8	16.9	9.09	1.3	19.27	1.7	12.55	2.6
			Total	33	51.71	15.1	110.0	7.6	68.3	10.0	9.27	1.1	18.67	1.4	11.39	2.1
			F[b]		7.75**		7.47**		1.29 n.s.		0.42 n.s.		2.06 n.s.		3.50*	

[a] Only 47 tails were measured in *A. cahirinus* others being broken (N = 10, 5, 6, 4, 7, 9, 6 in each population, respecitvely) and 16 tails in *A. russatus* (N = 4, 8, 4 respectively). – [b] F represents the statistic of ANOVA; degrees of freedom for *A. cahirinus* 6,72 except in tail and tail/body ratio where they were 6,40; and for *A. russatus* 2,30, and for tail and tail/body 2,13. * = $p < 0.05$; ** = $p < 0.01$; $p < 0.001$; n.s. = non significant.

Table 2a. **continued**

Species	2n	Pop. No.	Locality	Sample size N	Tail/Body[a] Mean	Tail/Body[a] S.D.	Forefoot/Body Mean	Forefoot/Body S.D.	Hindfoot/Body Mean	Hindfoot/Body S.D.	Ear/Body Mean	Ear/Body S.D.
					Length ratios							
A. cahirinus	38	1	Hurfeish	12	0.936	0.068	0.086	0.007	0.176	0.011	0.118	0.011
		2	Bet Oren	11	0.861	0.063	0.082	0.009	0.163	0.007	0.101	0.008
		3	Jerusalem	11	0.913	0.062	0.080	0.008	0.169	0.013	0.121	0.008
		4	Mitzpe Ramon	11	0.937	0.081	0.081	0.006	0.157	0.019	0.144	0.027
		5	Timna	12	1.122	0.099	0.096	0.015	0.188	0.010	0.141	0.012
	36	6	Neviot	15	1.100	0.079	0.095	0.015	0.184	0.014	0.148	0.013
		7	Santa Katharina	8	1.020	0.049	0.087	0.006	0.186	0.014	0.150	0.008
			Total	80	0.995	0.115	0.087	0.012	0.175	0.017	0.133	0.022
			F[b]		12.08***		4.48***		9.33***		17.16***	
A. russatus	66	8	Mitzpe Ramon	7	0.639	0.058	0.081	0.006	0.160	0.010	0.102	0.017
		9	Neviot	15	0.666	0.036	0.090	0.013	0.177	0.016	0.100	0.008
		10	Santa Katharina	11	0.551	0.136	0.079	0.008	0.168	0.008	0.109	0.018
			Total	33	0.631	0.086	0.085	0.011	0.170	0.014	0.103	0.014
			F[b]		3.11 n.s.		4.57*		4.38*		1.32 n.s.	

Table 2b. **Morphometrics of *Acomys cahirinus* and *Acomys russanus* accompanied by analysis of variance (ANOVA); Females**

Species	2n	Pop No.	Locality	Sample size N	Weight (g) Mean	Weight (g) S.D.	Body Mean	Body S.D.	Tail[a] Mean	Tail[a] S.D.	Forefoot Mean	Forefoot S.D.	Hindfoot Mean	Hindfoot S.D.	Ear Mean	Ear S.D.
							Length (mm)									
A. cahirinus	38	1	Hurfeish	7	42.94	5.1	108.3	5.9	100.2	3.0	9.14	0.7	18.14	2.8	13.57	2.1
		2	Bet Oren	11	43.45	7.5	108.8	6.6	98.0	5.2	9.27	0.8	18.55	0.7	11.55	0.7
		3	Jerusalem	6	32.20	5.9	100.0	7.8	96.8	6.1	8.33	0.8	17.83	1.0	12.67	0.5
		4	Mitzpe Ramon	15	47.67	8.2	111.3	7.5	105.8	6.7	9.07	0.5	17.67	2.1	16.80	2.6
		5	Timna	2	42.20	9.8	106.5	12.0	118.5	2.1	9.50	0.7	16.50	2.1	17.50	3.5
	36	6	Neviot	7	35.81	5.3	100.9	7.4	114.2	4.9	8.43	0.8	18.43	0.8	14.86	1.7
		7	Santa Katharina	5	34.48	6.8	103.4	7.2	107.5	10.6	9.00	0.7	19.00	0.7	15.40	0.9
			Total	53	41.40	8.7	106.8	8.0	103.8	8.4	8.96	0.7	18.11	1.7	14.23	2.5
			F[b]		5.44***		2.98*		8.35***		2.28 n.s.		0.91 n.s.		8.47***	
A. russatus	66	8	Mitzpe Ramon	4	59.73	11.0	104.3	9.4	74.5	2.1	8.50	1.2	18.75	1.0	10.25	1.0
		9	Neviot	8	43.24	8.5	103.8	9.5	73.4	3.5	9.13	0.6	18.63	0.9	10.88	0.6
		10	Santa Katharina	3	55.27	16.7	116.7	11.2	58.0	–	10.00	1.7	20.00	2.0	13.00	1.8
			Total	15	50.04	12.7	106.5	10.5	72.2	5.6	9.13	1.1	18.93	1.2	11.13	1.8
			F[b]		3.46 n.s.		2.05 n.s.		9.67**		1.67 n.s.		1.56 n.s.		2.68 n.s.	

[a] Only 42 tails were measured in *A. cahirinus* others being broken (N = 5, 9, 6, 13, 2, 5, 2 in each population, respectively), and 11 tails in *A. russatus* (2, 8, 1 respectively). – [b] F represents the statistic of ANOVA; degrees of freedom for *A. cahirinus* 6,46 except in tail and tail/body ratio where they were 6,35, and for *A. russatus* 2,12, and for tail and tail/body 2,8. * = $p<0.05$; ** = $p<0.01$; *** = $p<0.001$; n.s. = not significant.

Table 2b. **continued**

Species	2n	Pop. No.	Locality	Sample size N	Tail/Body[a] Mean	Tail/Body[a] S.D.	Forefoot/Body Mean	Forefoot/Body S.D.	Hindfoot/Body Mean	Hindfoot/Body S.D.	Ear Body Mean	Ear Body S.D.
					Length ratios							
A. cahirinus	38	1	Hurfeish	7	0.949	0.052	0.085	0.008	0.168	0.026	0.126	0.025
		2	Bet Oren	11	0.921	0.049	0.085	0.008	0.171	0.011	0.106	0.008
		3	Jerusalem	6	0.970	0.038	0.084	0.010	0.179	0.020	0.127	0.030
		4	Mitzpe Ramon	15	0.964	0.064	0.082	0.007	0.159	0.017	0.145	0.028
		5	Timna	2	1.119	0.106	0.089	0.004	0.157	0.038	0.164	0.015
	36	6	Neviot	7	1.148	0.101	0.084	0.012	0.184	0.015	0.147	0.008
		7	Santa Katharina	5	1.085	0.045	0.087	0.006	0.184	0.014	0.149	0.013
			Total	53	0.989	0.096	0.084	0.008	0.170	0.020	0.134	0.025
			F[b]		9.89***		0.47 n.s.		2.56*		6.85***	
A. russatus	66	8	Mitzpe Ramon	4	0.738	0.031	0.082	0.015	0.181	0.015	0.099	0.010
		9	Neviot	8	0.713	0.075	0.089	0.011	0.181	0.015	0.106	0.014
		10	Santa Katharina	3	0.479	–	0.086	0.011	0.172	0.006	0.110	0.022
			Total	15	0.696	0.097	0.086	0.012	0.179	0.013	0.105	0.014
			F[b]		5.19*		0.41 n.s.		0.55 n.s.		0.59 n.s	

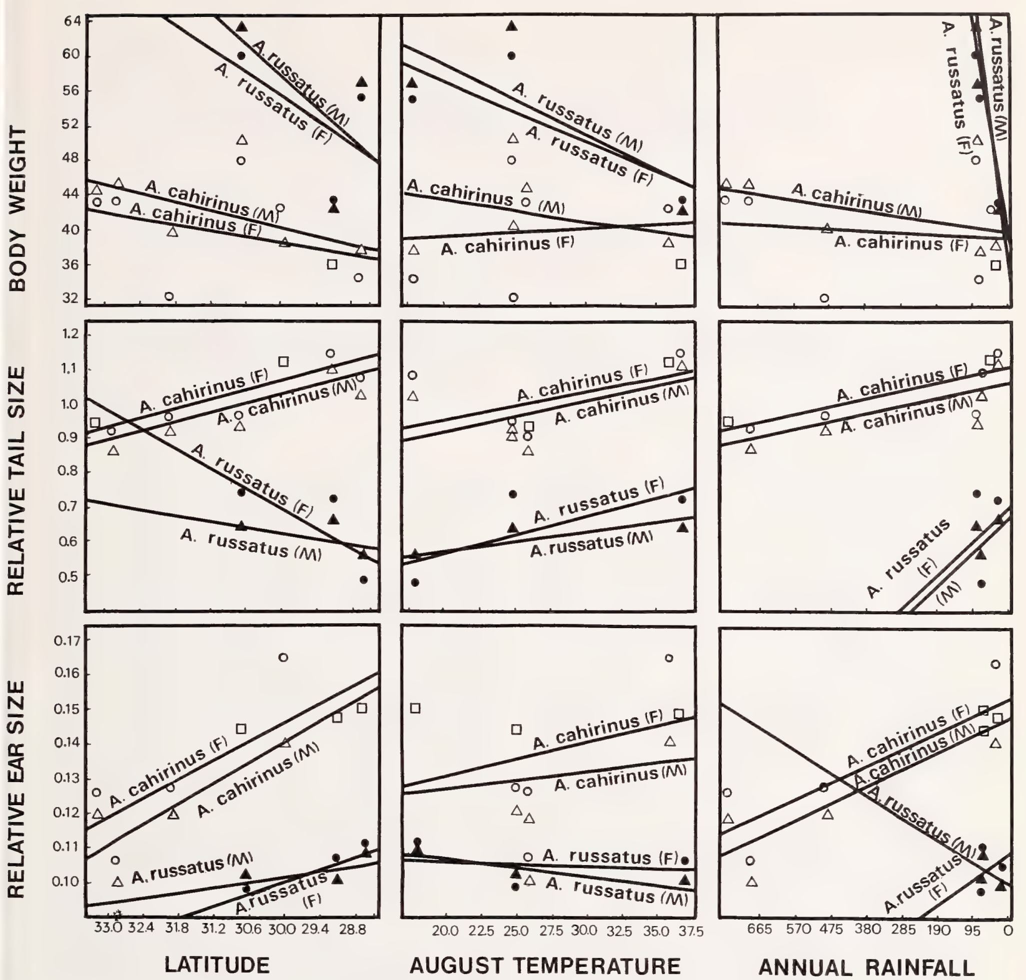


Fig. 2. Regressions of body weight and of relative ear and tail size of *Acomys cahirinus* and *A. russatus* on latitude, August temperature and annual rainfall. △ Population mean of males of *Acomys cahirinus*, ○ population mean of females of *Acomys cahirinus*, ▲ population mean of males of *Acomys russatus*, ● population mean of females of *Acomys russatus*, □ both sexes of *Acomys cahirinus*, (M) males, (F) females

figures in parentheses are Pearsonian r's for all 7 localities of *Acomys*. All 3 temperature variables, Tm, Tj and Ta, are highly correlated (0.88–0.97); Al and Tm (−0.97); Rn and Ta (−0.29); Rn and Hu (0.92); Ev and Ta, Rn and Hu (0.55, −0.86, −0.94, respectively). The low correlation between Rn and temperature is due to the reversed temperature trend in Santa Katharina. When the latter locality is excluded, the correlation between Rn and temperature is negatively high as usual across the studied area (r between Rn and the temperature variables are from −0.67 to −0.86).

In general, rainfall increases and temperature decreases northward with latitude; r (Rn–Lt) = 0.94; N = 7; and r (Tj–Lt) = −0.93 for 6 localities excluding Santa Katharina. In other words, aridity increases southward toward the Negev and Sinai deserts. Tm and Hu were eliminated from the multiple regression analysis in order to reduce the level of intercorrelations between the environmental variables.

Table 3. **Pearson correlation between morphology and climatic variables in *Acomys cahirinus* 7 populations**[1]

Variable	Sex	Geographical			Ecogeographical variables					
					Temperature			Water availability		
		Longitude (Ln)	Latitude (Lat)	Altitude (Al)	Annual (Tm)	Jan. (Tj)	Aug. (Ta)	Annual rainfall (Rn)	Midday humidity (Hu)	Evapo-ration (Ev)
Body weight	♂♂	.404	.600	−.005	−.696	−.547	−.762º	.395	.632	−.726º
	♀♀	.323	.361	−.251	−.170	−.139	−.232	.125	.343	−.323
Body length	♂♂	.174	.599	.109	−.616	−.469	−.784º	.550	.803*	−.788*
	♀♀	.235	.399	−.021	−.325	−.301	−.385	.211	.418	−.442
Tail length	♂♂	−.520	−.850*	−.181	.861*	.903*	.845*	−.908**	−.886**	.921**
	♀♀	−.375	−.765*	−.260	.884*	.832*	.905*	−.827*	−.856*	.923**
Forefoot length	♂♂	−.173	−.263	−.480	.781º	.659	.703	−.274	−.235	.501
	♀♀	.077	.159	.016	.025	−.125	.009	.069	.142	−.092
Hindfoot length	♂♂	−.485	−.308	.304	.490	.195	.511	−.030	−.237	.359
	♀♀	−.506	−.037	.554	−.267	−.209	−.330	.231	.164	−.192
Ear length	♂♂	−.726º	−.852*	.364	.397	.627	.361	−.894**	−.803*	.625
	♀♀	−.352	−.707º	.023	.542	.561	.589	−.835*	−.815*	.721º
Tail/body ratio	♂♂	−.372	−.783*	−.202	.874*	.781º	.947**	−.774*	−.906**	.959***
	♀♀	−.537	−.873**	−.097	.925**	.863*	.968***	−.803*	−.934**	.991***
Forefoot/body ratio	♂♂	−.213	−.584	−.371	.892*	.717	.966**	−.562	−.719º	.862
	♀♀	−.202	−.305	.031	.526	.247	.581	−.202	−.360	.474
Hindfoot/body ratio	♂♂	−.357	−.604	.041	.721	.481	.863*	−.440	−.726º	.779*
	♀♀	−.492	−.303	.367	.094	.114	.095	−.010	−.184	.184
Ear/body ratio	♂♂	−.660	−.916**	.237	.589	.712	.619	−.932**	−.945***	.807*
	♀♀	−.431	−.819*	.047	.634	.648	.699	−.889**	−.929**	.838*

º = $p < 0.10$, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$. [1] The correlations with the 3 temperature variables were performed on 6 populations only, excluding Santa Katharina.

Morphological correlates with climate

As can clearly be seen in Table 3, high and significant correlations, above those expected by chance, relate morphometrics and climatic factors. Body size significantly decreases (r, for males, = −0.79; $p < 0.05$) southward with evaporation whereas the relative tail size in males increases southward with evaporation ($r = 0.96$; $p < 0.001$). Even single climatic factors explain significantly the morphological variance in body ratios, but much more of the variance is explained by two or three variable combinations (see later, multiple regression analysis, Table 5).

Morphological correlates with allozymes

The frequencies of some allozymes show significant correlations with morphometric means (Table 4). The analysis is based on the assumption that there is no real difference in allozyme frequencies between the sexes. The reliance on male morphometrics stems from their better sampling. Because of the high correlation between the morphometrics of both sexes, the analysis of females gave similar results. The following alleles showed significant correlations with morphometrics, the numbers in parentheses indicate the number of body variables correlated with the alleles: Aat-1^{a} (3); Est-2^{a} (2); Est-2^{c} (1); Est-3^{a} (1); Est-5^{b} (3); Est-6^{b} (1) and Est-7^{b} (2). In addition, in females only: Pept-2^{c} ($r = -0.81^{*} = p < 0.05$ with forefoot); Est-6^{c} ($r = 0.78^{*}$ with ear, and $r = -0.82^{*}$ with hindfoot-body ratio). It thus appears that allozymic and morphological diversities are at least partly significantly correlated, primarily with the allele frequency in several esterase loci. Both allozymic and morphological variations are correlated with environment.

Multiple regression analysis

A test of the best predictors of the morphological variables of the populations of the *A. cahirinus* complex was conducted by stepwise multiple regression analysis, MR (SPSS-x 1986), employing the aforementioned variables as dependent variables and ecogeographic factors as independent variables. The results are given in Table 5. A substantial

Table 4. **Pearsonian correlations between male morphometric means and allozymic frequencies in 7 populations of the *Acomys cahirinus* complex**

Variable	Aat-1^{a}	Est-2^{a}	Est-2^{c}	Est-3^{a}	Est-5^{a}	Est-5^{b}	Est-6^{b}	Est-7^{b}	Ao^{a}
Weight	–	–	–	–	–	–	–	–	0.925^{e}
Body length	0.715^{e}	–	–	–	–	–	–	–	–
Tail length	-0.795^{*}	–	–	–	–	-0.825^{*}	-0.732^{e}	0.973^{**}	–
Forefoot length	–	–	-0.864^{*}	0.800^{*}	–	–	–	0.817^{e}	–
Hindfoot length	–	0.672^{e}	-0.681^{e}	–	–	–	–	–	–
Ear length	–	–	–	–	0.744^{e}	-0.808^{*}	-0.746^{e}	0.827^{e}	–
Tail/Body ratio	-0.870^{*}	0.743^{e}	–	–	–	–	-0.685^{e}	–	–
Forefoot/Body ratio	-0.913^{**}	–	–	–	–	–	–	–	–
Hindfoot/Body ratio	–	0.801^{*}	–	–	–	–	–	–	–
Ear/Body ratio	–	–	–	–	–	-0.812^{*}	-0.795^{*}	0.977^{**}	–

Aat-1 = aspartate aminotransferase, Est-2-7 = Esterases 2–7, Ao = aldehyde oxidase. All upperscripts a–c are allele designations. ^{e} = $p < 0.10$, * = $p < 0.05$, ** = $p < 0.01$, – = non significant correlations.

Table 5. **Coefficients of multiple determination (R^2) employing as dependent variables 6 morphological variables and 4 morphological ratios of *Acomys cahirinus* and as dependent variables geographic + climatic, and climatic factors**

Variable	Stepwise model					
	Geographic + Climatic variables			Climatic variables		
Weight ♂♂	Same as for climatic variables			Ev 0.53º	EvRn 0.73º	EvRnTa 0.84
Body length ♂♂	Ev 0.62*	EvLn 0.72º	EvLnAl 0.95*	Ev 0.62*	EvRn 0.68º	EvRnTj 0.70
Tail length ♂♂	Same as for climatic variables			Ev 0.85**	EvRn 0.90*	EvRnTa 0.93*
Forefoot length ♂♂	Ta 0.39	TaLn 0.54	TaLnLt 0.85º	Ta 0.39	TaEv 0.43	TaEvRn 0.45
Hindfoot length ♂♂	Ln 0.24	LnRn 0.38	LnRnEv 0.83	Tj 0.20	TjTa 0.64	TjTaRn 0.65
Ear length ♂♂	Same as for climatic variables			Rn 0.80**	RnTa 0.90*	RnTaEv 0.91*
Tail/Body ratio ♂♂	Ev 0.92***	EvLn 0.96**	EvLnAl 0.98**	Ev 0.92***	EvTa 0.93**	EvTaTj 0.97*
Forefoot/Body ratio ♂♂	Ev 0.75*	EvLt 0.93**	EvLtAl 0.96*	EV 0.75*	EvRn 0.87*	EvRnTa 0.91*
Hindfoot/Body ratio ♂♂	Same as for climatic variables			Ev 0.58*	EvRn 0.80*	EvRnTj 0.94*
Ear/Body ratio ♂♂	Rn 0.87**	RnAl 0.90**	RnAlTa 0.94*	Rn 0.87**	RnTj 0.90**	RnTjTa 0.91*

Abbrev. of environmental variables: Ln = Longitude, Lt = Latitude, Al = Altitude, Ta = mean August temperature; Tj = mean January temperature, Rn = annual rainfall, Ev = annual evaporation. º = $p<0.10$, * = $p<0.05$, ** = $p<0.01$, *** = $p<0.001$.

amount of the geographic variation in body characters was explained by the climatic factors of water availability (evaporation and rainfall) and temperature. Note that the variance in body ratios, which represents the relative estimates of body extremities (tail, ear, fore- and hindfoot lengths) is significantly explained by a single factor (either evaporation or rainfall), but a two or three variable combination explains above 90 % of the variance.

Discussion

I will subdivide the discussion into tow parts, 1. general, including other examples of geographic variation of body size in both space and time across Israel and in other regions, and 2. specific, analysing the results of the *Acomys* complex.

General comments on body size and energetics

The usual explanation of the positive correlation of body weight with latitude in homoiotherms (Bergmann's rule) relates to the physics of heat exchange, providing a thermoregulatory device for conserving energy in colder climates by a larger body size, and dissipating energy in warmer climates by a smaller size. This interpretation of Bergmann's rule was criticized by Scholander (1955) on several grounds. First, many species did not follow the rule and those that did show clinal increases in weight were

physiologically unimportant. Second, many of the characters supposedly associated with the rule have no significance in heat exchange. The rule was also questioned when some poikilotherms reflected it (Ray 1960). Rensch (1932) concluded that when factors other than temperature affect body size the maximum is reached in the optimal portion of the species range. Mayr (1970) emphasized that diametrically opposed size trends occur in species differing in life cycle patterns, sexual maturity, and optimal habitats.

In a series of studies on the patterns and evolution of endothermy in the phylogeny of mammals and other vertebrates McNab (1970, 1971, 1974, 1979, 1980, 1983) has critically analysed the influence of body size on the energetics, food habits and population biology of mammals. In his analysis of the ecological significance of Bergmann's rule, McNab (1971) emphasized that those species which do conform to the Bergmann rule "are usually carnivores or granivores; a change in their body size reflects a change in the size of their prey. A latitudinal change in the size of available prey is due either to the distribution of the prey species or to the distribution of other predators utilizing the same prey species. Only the smallest species of a set of similar predators normally will conform to Bergmann's rule, and then only beyond the limits of distribution of the largest species. These changes in size seem to be another example of character displacement."

McNab concluded that Bergmann's rule usually is a special case of a more general phenomenon related to food frequency and its size and the presence of other species that utilize the same food resources. In a recent analysis McNab (1983) analysed the complex relationship between energetics and body size and the limits to endothermy. Most vertebrates follow a Kleiber relation down to a "critical" mass, below which the scaling of metabolism must be changed to ensure the maintenance of endothermy. Critical mass varies inversely with the level of energy expenditure. The perfection of endothermy may always require an evolutionary decrease in mass. These considerations may not only be true at higher taxonomic levels, but also intraspecifically.

Body size as a "niche difference"

Body size variation may permit the coexistence of close species, thus providing an important niche parameter. The reason is that different sized animals eat different sized foods, hence utilize differential resources, at least partly nonoverlapping in size, to allow coexistence (MacArthur 1972). Wilson (1975) describes patterns of convergence and divergence of body size unifying in his model seemingly contradictory concepts: 1. the concept that differences in body size promote a niche difference (Hutchinson 1959; Brown and Wilson 1956; Schoener 1965, 1967, 1970, 1974a, b; Grant 1968, 1972), and 2. the concept that differences in body size set up a competitive gradient whereby the larger can exclude the smaller (Brooks and Dodson 1965; Galbraith 1967).

Spatiotemporal variation in size of other rodents in Israel

Several studies analyse the spatial and temporal morphological variation in Israeli rodents. Size variation of *Meriones tristrami* was analysed by Chetboun and Tchernov (1983). Its size variation over the geographic range of Israel and northern Sinai and during the late Middle and Upper Quaternary of Israel is correlated with environmental factors. The allopatric fossil populations were found to fluctuate in accordance with Bergmann's rule (i.e., the maximum body size was obtained during colder phases). Recent populations did not show north-south body size gradient of high correlation with climatic factors. A sudden shift in body size of *M. tristrami* is observed when sympatry with its congener *M. sacramenti* occurs in the Coastal Plain, and another (and smaller) shift is noticeable when sympatry with a third congener *(M. crassus)* takes place in the Negev region. The allopatric convergence and sympatric divergence suggest an ecological interaction (character dis-

placement) among the congener species. A significant north-south increase in the relative volume of the bulla tympanica of *M. tristrami* is shown, with the mastoid portion playing the main role in geographic variation. The bulla volume is highly correlated with climatic factors and shows no divergent shifts within the sympatric region. It is suggested that in fossil populations the bulla tympanica can be used for evaluating palaeoclimatic fluctuations.

Size trends and Pleistocene paleoclimatic response of the murid genus *Apodemus* (subgenus *Sylvaemus*) were studied by Tchernov (1979). Eleven Pleistocene sites in Israel yielded samples of successive populations of *Apodemus*. Three species occur: two (*A. mystacinus* and *A. sylvaticus*) are continuously represented in the area, while the third, *A. flavicollis,* occurs only during colder periods. The separation of fossil populations is possible only on biometrical grounds. The observed distribution of coexisting populations revealed significantly different modes of each parameter, caused by strict ecological exclusion. Molars showed three well-defined morphological size-groups within each of the three species when they coexisted in closely related adaptive zones. Neither significant complication, simplification nor clinal variation occurred in tooth structure since early Middle Pleistocene.

In the Middle East three different lineages of *Apodemus,* which never overlapped in size, were present during the Middle and Upper Pleistocene. When all three species coexisted, parallel changes in size with time occurred in all of them simultaneously, apparently in accordance with Bergmann's rule. Yet when *Apodemus flavicollis* was temporarily eliminated from the scenario in warm periods, the other two species filled the vacated space independently of climate, and in contrast to Bergmann's rule. Two factors greatly affected the character displacement of the three chrono-species: interspecific competition and climate. As competitive exclusion of these three closely related species is and was heavy, it is suggested that no factor other than size was involved in their evolution during the last 700,000 years. The significant size changes of each of these lineages, with no overlap among them, were interpreted by correlations with climatic factors and by ecological exclusions.

In an extensive survey of faunal turnover and extinction rate in the Levant, Tchernov (1984) analysed size changes in the late Pleistocene and postglacial period. Size change is exemplified most drastically by postglacial radical dwarfing seen in several species of mammals in Israel: *Canis lupus, Ursus arctos, Sus scrofa,* and *Felis sylvestris* (Kurten 1965); *Spalax ehrenbergi* and *Microtus guentheri* (Tchernov 1968); *Gazella gazella, Vulpes vulpes,* and *Canis lupus* (Davis 1977). Davis showed that the Aurignacian wolf of Israel attained the same dimensions as the present population of southern Sweden. Differences in mean temperature (for the hottest or coldest months) between the two regions is around 15 °C. According to Davis (1977), dwarfing commenced within the Natufian period (10,000 to 12,000 B.P.) and was completed approximately during the Neolithic. It is obvious that a conspicuous climatic change took place in the eastern Mediterranean region, an effect not clearly shown by the mammalian fauna turnover.

A detailed analysis on differentiation of body size in general (Nevo et al. 1986) and on 42 skull and body characters (Nevo et al. 1988) have been conducted on the four chromosomal species (2n = 52, 54, 58 and 60) of subterranean mole rats of the *Spalax ehrenbergi* complex in Israel. For differentiation of body size, the weight of 1,653 subterranean mole rats comprising 12 populations of the four chromosomal species were analysed. The results indicated that there is a southward latitudinal gradient in body size. Northern animals living in cooler and more productive mesic environments are larger than southern animals living in warmer and less productive xeric environments. Body size is negatively correlated with temperature variables, and positively correlated with plant cover (reflecting productivity or food resources) and rainy days. The best predictors of body size, explaining up to 87 % of the variation in size included various combinations of

temperature variables and plant cover. The conclusions were that in both adaptation and speciation natural selection is a major agent of differentiation of body size in accordance with multiple factors, primarily temperature and food resources operating on the energetics balance.

In a complementary study (NEVO et al. 1988) the morphometrics of 327 adult subterranean mole rats comprising 44 populations distributed across the ranges of the four chromosomal species of the *Spalax ehrenbergi* superspecies in Israel has been studied on a total of 42 skull and body variables. The results indicated that climatic variable combinations of temperature and water availability explain a significant part of the variance of most skull and body variables. Morphological diversity displays a southward gradient of decreasing size in skull and body variables which are significantly explained by climatic selection (and indirectly by decreasing resource availability southward). Hence it is adaptive and explicable on even very low selective pressures over evolutionary time.

Geographic variation of decreasing body size southward occurs in Israel in other homoiotherm mammals (e.g., wolves, leopards and hedgehogs; in MENDELSSOHN 1982) and in birds (partridges; in NISANI 1974). In contrast, increase in body size southward occurs in some poikilotherms (e.g., toads; in NEVO 1972). The decrease in body size southward in mammals and birds may be due to the sole or combined effects of higher temperatures and lower productivity in the xeric southern Negev and Sinai deserts. The increase in size of toads southward may be due to the fact that larger toads, having a relatively smaller evaporative body surface area, are capable of withstanding longer periods of dessication and are therefore selectively superior in arid habitats.

Ecophysiological, genetical and morphological differentiation of spiny mice, *Acomys*

What are the evolutionary forces molding body size differentiation in spiny mice in Israel? I will first summarize the ecophysiological background structure, then discuss body size differentiation, relate it to allozymic diversity and assess the evidence indicating that natural selection is a major architect in population differentiation at both the molecular (i.e., genetic) and organismal (i.e., morphological) levels. See ENDLER (1986) for a critical review of natural selection in the wild.

Ecophysiological background

1. *A. cahirinus* is a climatically generalist species ranging over widespread mesic and xeric habitats across Israel and part of the Sinai, whereas *A. russatus* is a habitat specialist species restricted to extreme xeric desert conditions in these regions. Recently, *A. russatus* was described from the colder mountain tops of the southern Sinai desert at altitudes of up to 2650 m (HAIM and TCHERNOV 1974). Physiological analysis of the Sinai mountain top populations of *A. russatus* indicates that it is adapted to cold-stress physiology by means of a higher nonshivering thermogenesis (HAIM and BORUT 1974, 1975, 1981), whereas animals from the En-Gedi Judean Desert population were unable to produce enough heat to keep warm below 18 °C (SHKOLNIK and BORUT 1969), However, both species (*A. cahirinus* and *A. russatus*) are narrow-niched species restricted to life in rocky crevices where microclimatic conditions in their microhabitats are relatively constant and far more moderate than the surrounding climates (SCHMIDT-NIELSEN 1964; SHKOLNIK 1966); yet they differ in their thermal niche-breadth (see below).

2. *A. cahirinus* is able to regulate its body temperature over a much greater range of ambient temperatures than *A. russatus* in accordance with its larger habitat range (WEISSENBERG 1977; WEISSENBERG and SHKOLNIK 1977). However, *A. russatus* is physiologically better adapted for a diurnal life than nocturnal *A. cahirinus* by its ability to withstand

high ambient temperatures and generate less heat by metabolism, as well as its capacity to derive water from salty, succulent plants (Shkolnik and Borut 1969; Shkolnik 1971).

3. Both species are adapted to desert conditions through an adaptive syndrome which is more pronounced in *A. russatus* than in *A. cahirinus*. Their metabolic rates deviate from the expected based on weight, 34.5 % in the former and 13.5 % in the latter, thereby reducing the water required for evaporation. Likewise, maximum chloride concentration is higher in the urine of *A. russatus* (1500 mN), and it is almost twice that of *A. cahirinus*. Finally, both species have among the very highest mammalian urine concentration (4700–4800 mN; Shkolnik and Borut 1969).

4. High ratios of evaporative water loss characterize both species, but more so in *A. russatus* than in *A. cahirinus*, involving a high cutaneous water loss, about 60–70 % of the total. The high cutaneous water evaporation, particularly in diurnal *A. russatus*, allows it to dissipate at an ambient temperature of 30 °C, over the third of the heat it generates. This efficient cooling device through a high evaporation rate, which appears very high even when compared to other diurnal rodents, is compensated by a very efficient kidney, by food choice comprising snails and succulent plants and by behavioral adaptations of shade-path selection (Shkolnik 1971). All four ecophysiological factors suggest a tropical (hot and humid) evolutionary origin of Acomys (Shkolnik 1966), as is also substantiated by taxonomic (Ellerman and Morrison-Scott (1951), paleontological (Tchernov 1968, 1975, 1984) and cytogenetic (Warhman and Goitein 1972) studies.

Genetic and morphological patterns

The genetic differentiation and speciation in *Acomys* has been described elsewhere (Nevo 1985). Here I summarize the major genetic and morphological patterns. 1. Low levels of genic diversity (A, P, H) characterized *Acomys* but they were higher in the *A. cahirinus* complex than in *A. russatus*. 2. A substantial proportion of the variant loci, 40–50 % were either localized or sporadic, suggesting sharp local and regional differentiation of alleles across the mesic-xeric ranges of *Acomys* in Israel and Sinai. 3. In both *A cahirinus* and *A. russatus* the level of polymorphism and number of alleles increased southward with aridity. 4. Levels of A, P and H varied at enzyme and protein loci in different functional classes. Loci whose enzymes utilize substrates originating from the external environment are far more genetically diverse than loci whose enzymes utilize internal metabolites (Gillespie and Kojima 1968; Johnson 1974). Likewise, regulatory enzymes were more variable than nonregulatory enzymes (Johnson 1974). 5. Significant linkage disequilibria were found in *A. cahirinus* in three populations involving six alleles. 6. Deviations from Hardy-Weinberg equilibria owing to heterozygote paucity were found in eight populations involving five loci. 7. Significant heterogeneity between 14 polymorphic loci in their effective inbreeding coefficients suggest the operation of natural selection. This test was criticised on statistical grounds (Ewens and Feldman 1976) and I use it here only as a supportive, and not a conclusive result. 8. Polymorphism and allozymic variant at six polymorphic loci were correlated with and predicted by climatic factors of water availability and temperature. 9. Body characters vary significantly between geographical localities: Body weight and length decreased, whereas tail, ear and relative fore- and hindfoot lengths increased and were correlated significantly with aridity and temperature. 10. Morphology was found to be partly correlated with allozymic variation. 11. Genetic patterns of *A. cahirinus* and *A. russatus* varied in three sympatric localities. 12. Mean genetic distance, D, was very small within *A. cahirinus* (2n = 38 and 2n = 36), and within *A. russatus*. It was also very small between the karyotypes of *A. cahirinus* (2n = 38 and 2n = 36), but high between the *A. cahirinus* complex and *A. russatus*.

Adaptive differentiation of body size in spiny mice

The interspecific size differences between nocturnal *A. cahirinus* and diurnal *A. russatus* may relate to their striking pattern of competitive exclusion (Shkolnik 1966, 1971) which results in opposed patterns of circadian activity. This variation of body size between the species may represent niche differences (see Wilson 1975). The heavier body weight of *A. russatus*, as compared with *A. cahirinus* (Table 2) may be associated with its diurnal life, where a relatively small surface to volume ratio may be adaptively superior in dry and high-radiation environments.

In general, in both *A. cahirinus* and *A. russatus*, sizes decrease and extremities increase with aridity and temperature (Fig. 2). These two trends reflect a positive correlation of weight with latitude (Bergmann's rule) and a negative correlation of body extremities with latitude (Allen's rule). Both patterns appear to better adapt *Acomys* to a progressively increasing heat load southward by improving its thermoregulation capacity through larger dissipating heat surfaces. Most fossorial mammals conform to these trends, although the interpretation of the trend in other mammals is often complex, and may involve interspecies interaction or character displacement (e.g. McNab 1979; Chetbourn and Tchernov 1983; Tchernov 1979; Wilson 1975).

Although one could suggest character displacement as a factor involved in body size differentiation of spiny mice, it appears very unlikely. In all three populations where both *A. cahirinus* and *A. russatus* coexist (localities 4–8, Mitzpe Ramon; 5–9, Neviot; and 7–10, Santa Katharina) the size difference appears to reflect an extension of general regional gradient of each of the species, rather than local character displacement, as is evident by the general ranking pattern in each of the species and in both sexes, i.e., decrease in size southward from the Central Negev desert (Mitzpe Ramon) to the Sinai desert (Neviot). The increase in size of *A. russatus* in both sexes at the mountaintop of Sinai (Santa Katharina) appears to support the thermoregulatory hypothesis. The contribution of a bigger body size to thermoregulatory efficiency in mountaintop colder environments complements the physiological adaptation by nonshivering thermogenesis of this population (Haim and Borut 1974, 1975, 1981).

The involvement of natural selection in genetic and morphological population differentiation is suggested by points number 1–11 mentioned above for both allozymes and body characters, which are intercorrelated and are explicable at least partly by the environment. Neither gene flow nor genetic drift can explain satisfactorily the genetic and morphological patterns found. If gene flow was a major factor, sporadic and localized alleles would not comprise about half of the variant alleles, and clines should have been more abundant. If genetic drift was a major factor, fixation of alternative alleles should have been more pronounced within the *A. cahirinus* complex and allele distribution would not be explained, at least partly, by climatic factors. Likewise, it is unlikely that small size population effects are responsible for the regional patterns. Both species are very abundant in the continuous rocky habitats across Israel and parts of Sinai. The intercorrelation between allozymic and morphological diversities reinforce their adaptive component.

In sum the morphological differentiation of body size, like the genetic one (Nevo 1985) appears to relate to environmental factors. Climatic factors appear substantial in molding body size as a contributor to thermoregulatory efficiency interacting with genetic, physiological and behavioral factors to optimize the energetics balance. Additional factors such as decline in resource availability southward may also contribute to the decrease in body size toward the hot Negev and Sinai deserts. It is noteworthy that desert rodents in Israel show a peaked curve of diversity over productivity, drastically declining in the deep desert (Abramsky and Rosenzweig 1984).

While in general temperature and aridity (i.e., lower productivity) increase southward across the *Acomys* range, they are correlated and impossible to disentangle. Partial

separation of both factors may be achieved between hot and arid Neviot populations and cold and arid Santa Katharina populations, both in the Sinai desert. Here, while aridity (hence productivity) is similar, temperature differences are extreme. Therefore, size differentiation between both sites appear largely to be determined by temperature, in accordance with the Bergmann rule. This is observed primarily in *A. russatus*. However, the relative importance of declining food resources in the southward decrease in size remains to be further evaluated by critical, specifically designed experiments.

Natural selection appears to be a major architect of size as well as allozyme (Nevo 1985) differentiation in spiny mice and of their interaction. A critical discussion of the operation of natural selection in natural populations has been presented by Manly (1985) and Endler (1986).

Evolutionary history and the rate of morphological differentiation

The evolutionary center of origin of spiny mice based on taxonomic grounds (Ellerman and Morrison-Scott 1951; Wahrman and Goitein 1972 and references therein) is the Ethiopian Region, and Israel represents a northern extension from this center. The African genus *Acomys* existed apparently in the Near East since the Pliocene, as it is found in Cyprus which separated from the mainland not later than the early pleistocene. This Pliocene ancestor presumably radiated into several closely related species (e.g. Atallah 1967). No *Acomys* remains were found however, in the Pleistocene of Israel until as late as the Aurignacian in the upper Palaeolithic, i.e., some 20,000 years ago (Tchernov 1968, 1975). *A. cahirinus* is a recent colonizer to the mesic but deforested Mediterranean region, particularly in the Epipaleolithic period, i.e., 15,000 B.P. Noteworthy, in the Mediterranean region *A. cahirinus* occurs primarily on warm and dry south-facing wadi slopes, presumably reflecting its derivation from steppic or desert origins, whereas the cooler and more humid north-facing slopes in Mount Carmel, for example, are primarily inhabited by the European *Apodemus* (Nevo, unpubl.). *A. russatus* may have originated in the extreme southwest Asiatic arid zones.

The three chromosomal forms of *Acomys* in Israel, *A. cahirinus* (2n = 38, 36) and *A. russatus* (2n = 66) appear to represent two speciation events: an old and a recent one. This deduction is based on both karyotypic differentiation (Wahrman and Zahavi 1953) and genetic distances (Nevo 1985). The genetic distance separating *A. russatus* and *A. cahirinus* is D = 0.30. A rough evolutionary divergence time for a pair of species estimated from electrophoretic data based on their genetic distance can be obtained by $t = 5 \times 10^6 D$ (Nei 1975). On this basis, *A. russatus* and *A. cahirinus* separated 1,500,000 ± 50,000 years ago. On the same basis, and in sharp contrast to this older speciation event, the karyotypic differentiation within *A. cahirinus* occurred 115,000 ± 40,000 years ago. This figure is in accordance with the fossil record which reveals *A. cahirinus* in Israel only as late as 20,000 years ago (Tchernov 1975). It supports the hypothesis that the Israeli form of *A. cahirinus* (2n = 38) has probably been derived from the Sinaitic form (2n = 36) through fission of one metacentric chromosome, rather than the reversed, cytologically simpler process (Wahrman and Goitein 1972).

The evolutionary recency of the *Acomys cahirinus* complex in Israel, i.e., 20,000 years, suggests that natural selection must have been instrumental in driving a relatively high evolutionary rate of size differentiation.

Acknowledgements

I thank the late M. Avrahami, S. Mendlinger and G. Heth for field assistance; Ch. Alkalay for laboratory assistance; M. Haber and A. Beiles for statistical assistance; D. Adler for commenting on the manuscript, and H. Waelder for the german translation of the abstract. Special thanks are due to A. Beiles for many stimulating discussions as well as for valuable advice for improvement of the

manuscript. This research was supported by grants from the United States-Israel Binational Science Foundation (BSF), the Israeli Discount Bank Chair of Evolutionary Biology and the "Ancell-Teicher Research Foundation for Genetics and Molecular Evolution" established by FLORENCE and THEODORE BAUMRITTER of New York.

Zusammenfassung

Natürliche Selektion in der Differenzierung von Körpermaßen bei der Stachelmaus, Acomys

Untersucht und miteinander verglichen wurden 181 Stachelmäuse des Genus *Acomys* von 7 Lokalitäten aus Israel und dem Sinai. Diese Tiere entsprechen 3 Karyotypen (2 Arten), welche 5 Populationen von *Acomys cahirinus* (2n = 38), 2 Populationen von *A. cahirinus* (2n = 36) und 3 Populationen von *A. russatus* (2n = 66) umfassen. Jede Population von *A. russatus* ist mit einer von *A. cahirinus* sympatrisch. Die 7 Lokalitäten erstrecken sich von Norden nach Süden und entsprechen Regionen mit schnittweise zunehmender Aridität. Die Ergebnisse der Untersuchungen zeigen: 1. Die Tiere der verschiedenen Lokalitäten unterscheiden sich in den erfaßten körperlichen Merkmalen signifikant voneinander. In Übereinstimmung mit der Bergmann'schen Regel zeigen Körpergewichte und -längen Abnahmen mit zunehmender Aridität, die absoluten Längen von Schwanz und Ohr sowie die relativen von Vorder- und Hinterfuß nehmen hingegen allgemein zu. 2. Die morphologischen Besonderheiten sind teilweise korreliert mit enzymatischen Variationen. Die Beziehungen zwischen geographischen Faktoren sowie klimatischen Besonderheiten und morphologischen Unterschieden bei *Acomys* in Israel und dem Sinai zeigen an, daß die natürliche Selektion als wichtigster Faktor für die Differenzierungen der Körpermaße angesehen werden muß. Diese Differenzierungen tragen bei zur Verbesserung der Thermoregulation. Durch sie wird die Energiebalance optimiert.

Literature

STATISTICAL PACKAGE FOR THE SOCIAL SCIENSES (SPSS-x) (1986): User's Guide, 2nd Ed. New York: McGraw Hill.

ABRAMSKY, Z.; ROSENZWEIG, M. L. (1984): Tilman's predicted productivity-diversity relationship shown by desert rodents. Nature **309**, 150–151.

ATALLAH, S. I. (1967): A new species of spiny mouse *(Acomys)* from Jordan. J. Mammalogy **48,** 258–261.

BROOKS, J. L.; DODSON, S. I. (1965): Predation, body size, and composition of plankton. Science **150,** 28–35.

BROWN, W. L.; WILSON, E. O. (1956): Character displacement. Syst. Zool. **5,** 49–64.

CHETBOUN, R.; TCHERNOV, E. (1983): Temporal and spatial morphological variation in *Meriones tristrami* (Rodentia: Gerbillidae) from Israel. Isr. J. Zool. **32,** 63–90.

CLUTTON-BROCK, T. H.; HARVEY, P. H. (1983): The functional significance of variation in body size among mammals. In: Advances in the Study of Mammalian Behavior. Ed. by J. F. EISENBERG and D. G. KLEIMAN. Shippensburg, PA, USA: Am. Soc. Mammologists, Spec. Publ. **7,** 632–663.

DAVIS, S. (1977): Size variation of the fox *Vulpes vulpes* in the Palaearctic region today and in Israel during the late Quaternary. J. Zool. (Lond.) **182,** 343–351.

EISENBERG, J. F. (1981): The Mammalian Radiations. Chicago: University of Chicago Press.

ELLERMAN, J. R.; MORRISON-SCOTT, T. C. S. (1951): Checklist of Palaearctic and Indian Mammals, 1758 to 1946. London: British Museum.

ENDLER, J. A. (1986): Natural Selection in the Wild. Princeton, NJ: Princeton University Press.

EWENS, W. J.; FELDMAN, M. W. (1976): The theoretical assessment of selective neutrality. In: Population Genetics and Ecology. Ed. by S. KARLIN and E. NEVO. New York: Academic Press. 303–337.

GALBRAITH, M. G. JR (1967): Size selective predation on *Daphnia* by rainbow trout and yellow perch. Trans. Amer. Fisheries Soc. **96,** 1–10.

GILLESPIE, J. H.; KOJIMA, K. (1968): The degree of polymorphism in enzymes involved in energy production compared to that in nonspecific enzymes in two *Drosophila ananassae* populations. Proc. Nat. Acad. Sci. **61,** 582.

GRANT, P. R. (1968): Bill size, body size, and the ecological adaptations of bird species to competitive situations on islands. Syst. Zool. **17,** 319–334.

— (1972): Interspecific competition among rodents. Ann. Rev. Ecol. Syst. **3,** 79–106.

HAIM, A.; BORUT, A. (1974): Differences in heat production among populations of the golden spiny mouse, *Acomys russatus*. Isr. J. Med. Sci. **10,** 286.

— — (1975): Size and activity of a cold resistant population of the golden spiny mouse *Acomys russatus*: Muridae. Mammalia **39,** 605–612.

— — (1981): Heat production in golden spiny mice *Acomys russatus* from two extreme habitats. J. Comp. Physiol. **142,** 445–450.

HAIM, A.; TCHERNOV, E. (1974): The distribution of myomorph rodents in the Sinai peninsula. Mammalia **38,** 201–223.
HUTCHINSON, G. E. (1959): Homage to Santa Rosalia, or why are there so many kinds of animals? Amer. Nat. **93,** 145–159.
JOHNSON, G. E. (1974): Enzyme polymorphism and metabolism. Science **184,** 28–37.
KURTEN, B. (1965): The carnivora of Palestine caves. Acta. Zool Fennica **107,** 1–74.
MACARTHUR, R. H. (1972): Geographical Ecology. New York: Harper and Row.
MANLY, B. F. J. (1985): The Statistics of Natural Selection. London: Chapman and Hall.
MAYR, E. (1970): Populations, Species and Evolution. Cambridge, MA: Belknap Press.
MCNAB, B. K. (1970): Body weight and energetics of temperature regulation. J. Exp. Biol. **53,** 329–348.
— (1971): On the ecological significance of Bergmann's rule. Ecology **52,** 845–854.
— (1974): The energetics of endotherms. Ohio J. Sci. **74,** 370–380.
— (1979): The influence of body size on the energetics and distribution of fossorial and burrowing mammals. Ecology **60,** 1010–1021.
— (1980): Food habits, energetics and the population biology of mammals. Amer. Nat. **116,** 106–124.
— (1983): Energetics, body size and the limits to endothermy. J. Zool. (Lond.) **199,** 1–29.
MENDELSSOHN, H. (1982): Wolves in Israel. In: Wolves in the World. Ed. by F. H. HARRINGTON and P. C. PAQUET. New Jersey: Noyes Publ. 173–197.
NEI, M. (1975): Molecular Population Genetics and Evolution. Amsterdam: North Holland Publ. Co.
NEVO, E. (1972): Climatic adaptation in size of the green toad *(Bufo viridis).* Isr. J. med. Sci. **8,** 1010.
— (1985): Genetic differentiation and speciation in spiny mouse, *Acomys.* Acta Zool. Fenn. **170,** 131–136.
NEVO, E.; BEILES, A.; HETH, G.; SIMSON, S. (1986): Adaptive differentiation of body size in speciating mole rats. Oceologia **69,** 327–333.
NEVO, E.; TCHERNOV, E.; BEILES, A. (1988): Morphometrics of speciating mole rats: Adaptive differentiation in ecological speciation. Z. zool. Syst. Evolut-forsch. **26,** 286–314.
NISANI, R. (1974): Geographic variability of the partridge *Alectoris chukar* and Bergmann rule. M. Sc. Thesis. Hebrew University, Jerusalem (in Hebrew).
RAY, C. (1960): The application of Bergmann's and Allen's rules to the poikilotherms. J. Morphol. **106,** 85–108.
RENSCH, B. (1932): Über die Abhängigkeit der Größe des relativen Gewichtes und der Oberflächenstruktur der Landschneckenschalen von den Umweltfaktoren. Z. Morphol. Ökol. Tiere **25,** 757–807.
SCHOENER, T. W. (1965): The evolution of bill size differences among sympatric species of birds. Evolution **19,** 189–213.
— (1967): The ecological significance of sexual dimorphism in size in the lizard *Anolis conspersus.* Science **155,** 474–477.
— (1970): Size patterns in West Indian *Anolis* lizards. II. Correlations with the sizes of particular sympatric species displacement and convergence. Amer. Nat. **104,** 155–174.
— (1974a): Resource partitioning in ecological communities. Science **185,** 27–39.
— (1974b): Some methods for calculating competition coefficients from resource spectra. Amer. Nat. **108,** 332–340.
SCHOLANDER, P. F. (1955): Evolution of climatic adaptation in homeotherms. Evolution **9,** 15–26.
SCHMIDT-NIELSEN, K. (1964): Desert Animals. Oxford: Clarendon Press.
SHIELDS, J. (1962): Monozygotic twins brought up apart and brought up together. Oxford: Oxford University Press.
SHKOLNIK, A. (1966): Studies in the comparative biology of Israel's two species of spiny mice (Genus *Acomys*). Ph. D. thesis, Hebrew University, Jerusalem (in Hebrew, with English summary).
— (1971): Diurnal activity in a small desert rodent. Intl. J. Biometeor. **15,** 115–120.
SHKOLNIK, A.; BORUT, A. (1969): Temperature and water relations in two species of spiny mice *(Acomys).* J. Mammalogy **50,** 245–255.
TCHERNOV, E. (1968): Succession of rodent faunas during the Upper Pleistocene of Israel. Hamburg und Berlin: Verlag Paul Parey
— (1975): Rodents faunas and environmental changes in the Pleistocene of Israel. The Hague: W. Junk Publ.
— (1979): Polymorphism, size trends and Pleistocene response of the subgenus *Sylvaemus* (Mammalia, Rodentia) in Israel. Isr. J. Zool. **28,** 131–159.
— (1984): Fauna turnover and extinction rate in the Levant. In: Pleistocene Extinction. Ed. by P. S. MARTIN and R. G. KLEIN. Tucson: Univ. of Arizona Press. 528–552.
WAHRMAN, J.; GOITEIN, R. (1972): Hybridization in nature between two chromosome forms of spiny mice. Chromosomes Today **2,** 228–237.
WAHRMAN, J.; ZAHAVI, A. (1953): Intra-generic difference in chromosome numbers of spiny mice (Rodentia: Murinae). Bull. Res. Coun. of Israel **3,** 265.

WEISSENBERG, S. (1977): Comparative physiology in two populations of common spiny mouse *(Acomys chahirinus)* from desert and mediterranean regions. M. Sc. Thesis. Tel Aviv University. (in Hebrew).

WEISSENBERG, S.; SHKOLNIK, A. (1977): Water turnover rates of two populations of spiny mice *(Acomys cahirinus)* from xeric and mesic habitats. Isr. J. Zool. **26**, 260.

WILSON, D. S. (1975): The adequacy of body size as a niche difference. Amer. Nat. **109**, 769–784.

Author's address: Prof. Dr. EVIATAR NEVO, Institute of Evolution, University of Haifa, Mt. Carmel, Haifa 31999, Israel

Z. Säugetierkunde 54 (1989) 100–106

ISSN 0044-3468

Growth of the garden dormouse (*Eliomys quercinus* Linnaeus, 1766) in southwestern Spain

By S. Moreno and E. Collado

Estación Biológica de Doñana Sevilla, Spain

Receipt of Ms. 3. 8. 1987

Abstract

Studied the growth of young dormice *(Eliomys quercinus lusitanicus)* from the SW of the Iberian Peninsula and compared with that of juveniles from Germany and El Pardo (Central Spain). Body measurements and weights were taken from suckling animals in captivity, and juveniles in the field (n = 57) and from scientific collections (n = 23). The mean daily growth, the average growth rate, and the mean percentage of adult size attained at different ages were calculated. The results show that, generally, the growth pattern is similar in the three populations studied. However, growth takes longer in the dormice from SW Spain which reach a greater size.

Introduction

Geographical variation in the body size of garden dormice (Rodentia, Gliridae) is very high. The average weight of adults ranges from less than 60 g in Central Europe (Kahmann and Staudenmayer 1969) to more than 170 g on Formentera Island, Spain (Kahmann 1970; Kahmann and Lau 1972).

In Europe, studies on garden dormouse growth have been conducted in Bavaria and Hessen, Germany (Kahmann and Staudenmayer 1969, 1970), in the French Alpes (Le Louarn and Spitz 1974), and in El Pardo, Central Spain (Palacios 1974). An analysis of growth in *quercinus* subspecies has been conducted by *Kahmann* and *Thoms* (1977).

In this paper the development and growth of *Eliomys quercinus lusitanicus,* one of the larger subspecies of garden dormouse (Petter 1961), is studied and compared with the available data on *Eliomys quercinus quercinus* in Bavaria and Hessen (Germany) and in El Pardo (Central Spain).

Material and methods

The garden dormice used for this study come from the SW of the Iberian Peninsula, from Doñana National Park (Huelva province) (37° N 0′, 6° 2 ′W) to Medina-Sidonia (Cádiz province) (36°, 30 ′N, 5° 35 ′W).

To study the development of the youngs from birth to weaning, 8 sucklings, born in captivity from a female captured in the field, were measured and weighted at 4–6 day intervals. For post-weaning growth studies, data from 57 juvenile individuals were obtained using a capture-mark-recapture technique twice a month during three consecutive years (1978–1981). Young specimens (Moreno 1984) from the Doñana Biological Station (CSIC) collection (n = 23) were also examined.

Standard body measurements were taken for each animal: head and body length (HBL), tail length (TL), ear length (EL), hindfoot length (HL) and weight (W). Weight of captured individuals were fitted to a Von Bertalanffy curve using Ricklefs' graphical method (1967). Ages for the individuals captured in the field were estimated when first captured by interpolation of their weight on a Gompertz curve fitted to the weights of the captive litter by Ricklefs' graphical method.

The growth rate has been expressed in three ways:

1. Average daily increase (I) in absolute values during a determined period of time:

$$I = (X_2 - X_1)/(t_2 - t_1)$$

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5402-0100 $ 02.50/0

where X_2 and X_1 are the means of each measurement at times t_2 and t_1, respectively (being t_2 the end of the period considered and t_1 the beginning).

2. Average daily growth-rate (R) according to the formula used by GURNELL and RENNOLL (1983):

$$R = (\ln X_2 - \ln X_1)/(t_2 - t_1)$$

This both indexes, I and R, allow comparison of growth rates independently of the frequency in which measurements are taken.

3. The proportion (P) with respect to adult size:

$$P = X_1/X$$

were X_1 is the measurement obtained at a certain time and X is the mean of the same measurement in adult specimens, obtained from KAHMANN and STAUDENMAYER (1969) for *quercinus* in Germany, from PALACIOS (1974) for *quercinus* in El Pardo and from MORENO (1984) for *lusitanicus.*

Results

Growth during lactation

At birth, the average weight of the laboratory litter specimens was 2.0 g, which is slightly under 2.32 g reported by PALACIOS (1974) in El Pardo and the 2.52 g and 2.45 g observed by KAHMANN and THOMS (1977) in Bavaria. The young were hairless, the eyes and auditory meatus were closed and the ears flattened against the head. On day 11, the ears were detached, the pelage appeared as distinct facial mask and dorsal fur was also beginning to appear. On day 17, the mask and tail markings were clearly defined, the dorsal fur growth was evident and signs of abdominal fur could be noticed. By day 21 the eyes and auditory meatus were open. One of the young showed aggressive behaviour. On day 36, the face, body and tail fur was almost completely grown, the animals were nutritionally independent and their aggressiveness was increasing.

Leaving aside the inaccuracy arising from taking measurements weekly, this pattern of development roughly coincides with that of other European populations of the species (VALENTIN 1980).

Table 1 shows measurement change during the first month of life. Table 2 shows the average daily increase (I), the average daily growth-rate (R) from day 11 to day 30 and the percentage of adult size (P) reached by day 30 in our population and those of Germany and Central Spain.

The greatest mean daily increase was observed in TL and the greatest mean daily growth-rate was observed in W. However, considering the proportion with respect to the

Table 1. **Body measurements (averages [X] and range [r]; weight [W], head-body length [HBL], tail length [TL], ear length [EL] and hind foot length [HL]) of eight captive suckling dormice *(Eliomys quercinus lusitanicus)* from SW Spain at different ages**

Age (days)		W	HBL	TL	EL	HL
11	X	6.3	53.1	29.7	6.6	10.9
	r	5.1–6.8	50.3–56.5	27.4–31.6	5.7–7.0	10.5–11.5
17	X	9.1	57.5	37.4	9.0	14.6
	r	8.5–10.5	54.3–60.0	35.5–40.0	8.4–9.7	13.9–15.5
21	X	11.4	67.7	45.9	10.5	17.2
	r	10.5–14.0	62.2–72.8	44.3–48.8	9.0–12.0	16.0–18.0
25	X	13.1	66.1	51.3	11.4	20.2
	r	12.3–15.5	62.2–73.0	47.9–58.0	9.2–13.1	17.3–18.9
29	X	14.4	70.3	59.3	13.7	20.9
	r	13.0–18.0	68.0–72.4	56.8–63.6	12.7–16.2	19.3–22.3

Table 2. **Average daily increase (I), average growth-rate (R), and mean percentage of adult size (P) of weight (W), head-body length (HBL), tail length (TL), ear length (EL) and hind foot length (HL) of suckling dormice *(Eliomys quercinus)***

	I			R			P		
	SWS	CS	G	SWS	CS	G	SWS	CS	G
W	0.45	0.33	0.77	0.046	0.044	0.057	11	22	41
HBL	0.96	1.15	1.43	0.015	0.017	0.023	47	–	–
TL	1.64	1.70	1.56	0.036	0.029	0.046	50	–	–
EL	0.39	0.45	–	0.038	–	–	54	–	–
HL	0.55	0.37	0.48	0.034	0.031	0.032	71	–	–

Data for the SW of the Iberian Peninsula (SWS) come from the present work and MORENO (1984). Data for Central Spain (CS) are taken from PALACIOS (1974) and for Germany (G) from KAHMANN and STAUDENMAYER (1969).

adult size, it is HL the parameter that most closely approaches the adult value and W the least. The weight gain fits a Gompertz curve with an asymptote of 100.3 g and a growth rate of 0.02879.

Growth after warning

The mean weight of the youngest individuals captured in the field was 20 g. The weight gains of a specimen captured in 9 consecutive trapping periods fit a Von Bertalanffy curve with an asymptote of 82 g. The mean growth-rate for all the individuals, considering this asymptote, is 0.00797, which results in a growth curve expressed by the equation:

$$W = 82 \times \left(1 - \frac{e^{-0.0179\,(t-39)}}{3}\right)^3$$

according to RICKLEFS's method, which would be representative of the growth in our population of garden dormice.

For the period between 28 and 70–80 days old, the average daily increases, the average daily growth-rate and the proportion with respect to adult size of W, HBL and HL are presented in Table 3. Weight has the lowest rate of change, reaching only 55.54 % of its definitive value when 70–80 days old. HL, reaches adult size when 80 days old, having a high percentage of adult size when 30 days old. HBL achieves from 80 % to 90 % of its definitive value when 70–80 days old.

In Figure 1, the proportion reached with respect to adult size in terms of HBL and W

Table 3. **Average daily increase (I), average daily growth-rate (R), and mean percentage of adult size (P) of the weight (W), head-body length (HBL) and hind foot length (HL) in *Eliomys quercinus lusitanicus* between 29 to 70–80 days old**

Method	Age (days)	W	HBL	HL
(I)	29–80	0.74	0.40	0.03
(R)	29–80	0.023	0.009	0.003
(P)	29–80	19	55	86
(P)	40–50	31	69	92
(P)	50–60	38	73	64
(P)	60–70	50	–	–
(P)	70–80	56	82	97

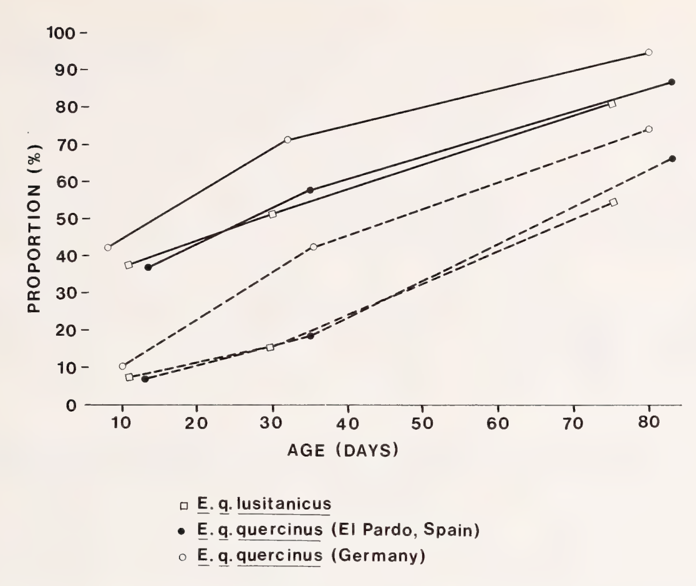


Fig. 1. Comparison of the relative growth (mean proportion of adult size) of the head-body length (continuous line) and weight (broken line) of the *lusitanicus* and *quercinus* (Central Spain and Germany) dormice subspecies. The data from Germany and Central Spain were obtained from Kahmann and Staudenmayer (1969) and Palacios (1974) respectively

for *Eliomys quercinus lusitanicus* is compared with *Eliomys quercinus quercinus* from Bavaria and Central Spain. Three facts can be noticed: 1. The two Spanish populations are similar but differ from the other; 2. German dormice take less time to reach adult size; 3. HBL reaches adult size quicker than W.

Differences related to time of birth and sex

Until now we have considered average values for our population, however as in the SW Iberia garden dormice has two distinct annual breeding periods (spring and autumn, Moreno 1984) a difference in growth-patterns between these two periods could be expected. Figure 2 shows some differences in weight increase between the young born in the first reproductive period (spring) and those born in the second (autumn). The growth of the spring-born youngs is relatively linear until they are 75–90 days old (when average weight is nearly 60 g and 60 % of the definitive value). The slope of the growth curve in the autumn-born youngs is smaller, linear until day 90 (when average weight of youngs 75–90 days old is 46 g and 49 % of the definitive value) decreasing by this time and returning to its former slope between day 150 and 180.

Although, the proportion of growth reached by spring-born youngs is relatively high, it does not approach that reached by young german dormice at same age (nearly 75 %).

No significant differences in growth rates were found between SW Iberian young males and females. This result was expected given the absence of sexual dimorphism in *Eliomys quercinus*.

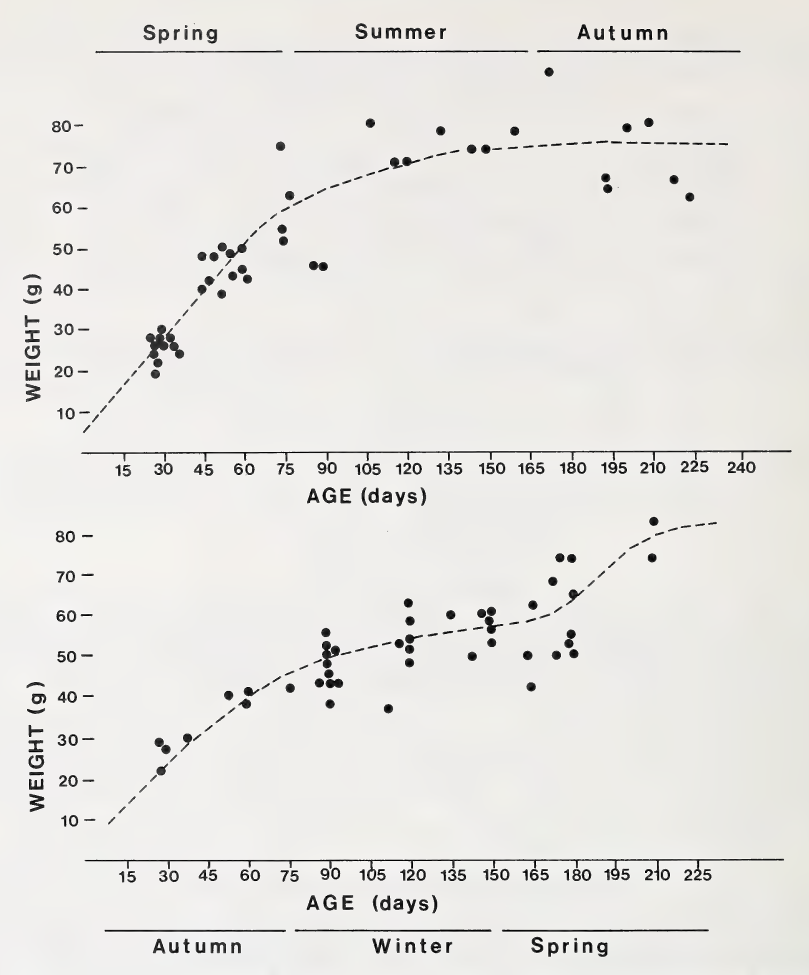


Fig. 2. Changes in weight of SW Iberian young garden dormice, *Eliomys quercinus lusitanicus*, (captured alive in the field) from their first capture, for dormice born in spring (top) and autumn (bottom). Lines were fitted by eye. Data coming from capture-recapture for 3 years pooled

Discussion

The results of this study reveal that during lactation and the onset of independent life, garden dormice from the SW of the Iberian Peninsula follow a growth pattern similar to that of dormice from Germany and Central Spain. The period of development of the SW Iberian subspecies, however, lasts longer, which may account for its larger size.

The relative growth rates of the El Pardo and SW Iberian specimens are similar at the same age, although the animals from Central Spain are smaller. This trend can be observed both in the development of the physiognomical characters before weaning as in the increase in weight and body measurements.

However, the relative growth rates of the german specimens are greater than those of the *lusitanicus* spanish ones. This difference is not only due to the influence of the *lusitanicus* autumn-born growth rates on the whole of the SW Iberian sample, as important

differences still appear when the growth of young spring-born is compared with that of the young german specimens.

Eisenberg (1981) has claimed that large-sized mammals need more time to reach adult size than smaller ones. According to this, the larger size of SW Iberian dormice could be the result of a longer growing period.

In fact this seems to be the case because the mildness of the winter in the study area allows the garden dormice to spend only a very short time in hibernation, and therefore also a very short time accumulating fat reserves to face hibernation energetic expenditures. In this way, the time spent by German dormice accumulating reserves and hibernating could be used by SW Iberian dormice to grow.

Different environmental conditions during the development seem to cause differences in growth patterns between spring and autumn-born youngs. The latter slowdown their growth during the winter, when they are 75–90 days old, and environmental conditions become adverse. 70 to 75 days later, at the beginning of the spring, they recover their initial growth rate.

A close relationship between environmental conditions and adult body size in garden dormice could also explain why *Eliomys quercinus* does not follow Bergman's rule in continental Europe, where average adult size decreases with latitude (Moreno in press).

However, this idea cannot be generalized, as north African garden dormice, genetically different from European ones (Delibes et al. 1980) are also of smaller size than the Spanish subspecies (Moreno and Delibes, 1981) although in theory the latitude allows a longer period of activity.

Clearly, ecological and genetical factors seem to be combined to determine the adult size of the different populations of dormice, and populations do not conform to simple zoogeographical rules.

Acknowledgements

We acknowledge Dr. M. Delibes and B. D. Cooke (Estatación Biológica de Doñana, CSIC) for reviewing the manuscript. The first author had a postdoctoral grant of the Consejo Superior de Investigaciones Científicas. Financial support was obtained from CSIC-CAYCIT (projet 944).

Zusammenfassung

Das Wachstum von südwestspanischen Gartenschläfern (Eliomys quercinus Linnaeus, 1766)

Das Wachstum südwestspanischer Gartenschläfer *(Eliomys quercinus lusitanicus)* wurde im Vergleich zu solchen aus Mittelspanien (El Pardo) und Deutschland untersucht. Zugrunde lagen Maße und Gewichte von 8 Nestlingen aus Gefangenschaft, 57 markierten und wiederholt gefangenen Jungtieren aus dem Freiland und 23 Jungtieren aus wissenschaftlichen Sammlungen. Die großen Gartenschläfer aus SW-Spanien und die kleineren aus Mittelspanien wachsen in gleichem Tempo aber gemeinsam langsamer als solche aus Deutschland, die etwa so groß werden wie die aus Mittelspanien.

Literature

Delibes, M.; Hiraldo, F.; Arroyo, J. J.; R-Murcia, C. (1980): Disagreement between morphotypes and kariotypes in *Eliomys* (Rodentia, Gliridae): the chromosomes of the Central Morocco garden dormouse. Säugetierkdl. Mitt. **28**, 289–292.

Eisenberg, J. E. (1981): The Mammalian Radiations. An Analysis of Trends in Evolution, Adaptation, and Behavior. London: The Athlone Press.

Gurnell, J.; Rennoll, K. (1983): Growth in field and laboratory populations of wood mice *(Apodemus sylvaticus)*. J. Zool. Lond. **200**, 355–365.

Kahmann, H. (1970): Der Gartenschläfer *Eliomys quercinus ophiusae* Thomas, 1925 von der Pityuseninsel Formentera (Morphometrie). Veröff. Zool. Staatssamml. München **14**, 75–90.

Kahmann, H.; Staudenmayer, T. (1969): Biometrische Untersuchung an zwei Populationen des Gartenschläfers *Eliomys quercinus* Linnaeus, 1766. Z. Säugetierkunde **34**, 98–109.

— — (1970): Über das Fortpflanzungsgeschehen bei dem Gartenschläfer *Eliomys quercinus* (Linnaeus, 1766). Säugetierkdl. Mitt. **18**, 97–114.

Kahmann, H.; Lau, G. (1972): Der Gartenschläfer *Eliomys quercinus ophiusae* Thomas, 1925 von der Pityuseninsel Formentera. II. Lebensraum. Veröff. Zool. Staatssamml. München **16**, 29–49.

Kahmann, H.; Thoms, G. (1977): Über Wachstum und Altern des europäischen Gartenschläfers, *Eliomys quercinus* (Linné, 1758). Säugetierkdl. Mitt. **25**, 81–108.

Le Louarn, H.; Spitz, F. (1974): Biologie et Ecologie du lérot dans les Hautes Alpes. La Terre et la Vie **28**, 544–564.

Moreno, S. (1984): Biometría, Biología y Dinámica Poblacional del lirón careto *Eliomys quercinus* (L.), en Doñana. Tesis doctoral. Univ. Granada.

Moreno, S.; Delibes, M. (1982): Notes on the Garden Dormouse (*Eliomys;* Rodentia, Gliridae) of Northern Morocco. Säugetierkdl. Mittl. **30**, 212–215.

Moreno, S. (1989): Variación geográfica de *Eliomys* en la Península Ibérica. Doñana Act. Vert. (in press).

Palacios, F. (1974): Contribución al estudio de la biología y ecología del liron careto, *Eliomys quercinus* Linnaeus 1766, en Iberia Central, Parte I: Crecimiento, Reproducción y Nidificación. Doñana Act. Vert. **1**, 171–231.

Petter, F. (1961): Les lérots des iles Baléares et de l'ouest de la région Méditerranéenne. Coll. Internat. C.N.R.S. **49**, 97–102.

Ricklefs, R. E. (1967): A graphical method of fitting equations to growth curves. Ecology **48**, 978–983.

Valentin, S. (1980): Etude du développement comportamental et anatomo-physiologique du lerot (*Eliomys quercinus* L.). Thèse le Doctorat de 3[e] cycle. Université de Franche-Comté, Besançon, 1983.

Authors' address: Sacramento Moreno and Enrique Collado, Estación Biológica de Doñana, Apartado 1056, E-41080 Sevilla, Spain

Z. Säugetierkunde 54 (1989) 107–110

ISSN 0044-3468

Comparative food habits of three carnivores in Western Sierra Madre, Mexico

By M. Delibes, Lucina Hernandez and F. Hiraldo

Estación Biológica de Doñana, Sevilla, Spain, Instituto de Ecología, México D.F., México and Museo Nacional de Ciencias Naturales, Madrid, Spain

Receipt of Ms. 22. 10. 1987

Abstract

Studied are the foods and diet partitioning of coyotes *(Canis latrans)*, gray foxes *(Urocyon cinereoargenteus)*, and coatis *(Nasua narica)* on the Western Sierra Madre, México, during summer 1981 and spring 1982. The three carnivores were generalist feeders, but coyotes ate mainly rodents, gray foxes fruit, and coatis arthropods. Trophic diversity and mean prey size were largest in the coyote, intermediate in the gray fox, and smallest in the coati. The least dietary overlap occurred between the coyote and the coati. Because prey abundance was the same for the 3 species, differences were assumed to reflect different feeding behaviour and ecology.

Introduction

The natural history of North American carnivores south of the United States is poorly documented. Information on the ecology of Mexican mammalian predators is limited, and most of the available data concern coyote-livestock problems in cattle ranges of Chihuahua (e.g. Pérez-Gutiérrez et al. 1982; Lafon 1983). The objectives of our study were to examine spring and summer food habits of coyotes *(Canis latrans)*, gray foxes *(Urocyon cinereoargenteus)*, and coatis *(Nasua narica)* in the oak-pine woodlands of the Western Sierra Madre and to compare the food-resource partitioning among these sympatric carnivores.

Study area

The study was done in the Biosphere Reserve of La Michilía, in the Mexican State of Durango (approx. 23°27′N, 104°18′W). Located in a transition zone ranging from high mountains to plateaus, the reserve has an average altitude of 2250 m and is an irregular high plain between 2 mountain ranges, the Sierras of Urica and Michis. Climate is semiarid temperate with summer rains (600 mm per year) and annual mean temperature of 19 °C (Gallina 1981). Vegetation is dominated by oak-pine forests (*Quercus* sp., *Pinus* sp.) with local patches of juniper (*Juniperus* sp.), manzanita thickets (*Arctostaphylos* sp.) and open grasslands. Besides the 3 carnivore species studied, mountain lions *(Felis concolor)*, bobcats *(Felis rufus)*, raccoons *(Procyon lotor)*, ringtails *(Bassariscus astutus)*, long-tailand weasels *(Mustela frenata)*, and 2 skunks *(Mephitis macroura, Conepatus mesoleucus)* also have been recorded in the area. Occasional wolf *(Canis lupus)* observations are recorded, and black bears *(Ursus americanus)* apparently were extirpated several years ago.

Material and methods

We collected 116 coyote, 99 gray fox and 87 coati faeces along dirt roads and paths of the reserve during July–August 1981 and April 1982. Faeces were identified to species based upon size, shape and odour (Murie 1974). We discarded very old faeces and those that could not be identified. Identification of prey items was made by comparison with a reference collection of hairs, teeth, seeds, etc. Occasional grasses and twigs occurring in faeces were not considered in the analysis. Mammal remains were identified to species when possible. We could not distinguish whether ungulates were killed by predators or consumed as carrion.

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5402-0107 $ 02.50/0

For each species, food items were quantified as: 1. number of occurrences (N), N_i = number of faeces where the i category of remains occurs, and 2. proportion of occurrence (PO), PO_i = number of faeces where the i category of remains occurs × 100/number of total occurrences of all categories in all examined faeces. This method does not reflect precisely the weight of ingested material, but indicates the relative role of the various items in the diet (Erlinge 1968).

We used G test (Sokal and Rohlf 1981) to compare the distribution pattern of each prey category in the diet of the 3 predators. When significant differences were found for 1 category, the observed frequency in each diet of this category was compared with the expected frequency under the null hypothesis, i.e., the prey category is equally frequent in the faeces of all 3 predators.

Trophic diversity (food-niche breadth) that measures the width of prey-use categories was estimated as (Levins 1968):

$$B = 1/\Sigma p_i^2$$

where B is food-niche breadth, and P_i is the relative occurrence of prey category i in the diet of a given species. This expression generates values from 1 to the number of used categories, 7 in this instance. Trophic similarity (food-niche overlap) of 2 species that measures the shared parts of their trophic niches was estimated as (Pianka 1973):

$$A = \Sigma p_i q_i / (\Sigma p_i^2 \Sigma q_i^2)^{1/2}$$

where A is food-niche overlap, and p_i and q_i are the relative occurrences of category i in the diet of the species p and q. This expression renders values ranging from 0, no overlap, to 1, complete overlap.

Results and discussion

The 3 carnivores were generalists. Ungulates, rabbits, rodents, reptiles, invertebrates, fruits, and berries all were found in the faeces we examined (Table 1). However, the major food items in the pooled faeces of the 3 species were fruit and berries (33.5 %), arthropods

Table 1. **Spring and summer diet of coyotes, gray foxes and coatis in the Western Sierra Madre, Mexico, based on the analysis of faeces (n)**

Food categories	Coyote (n = 116)		Gray fox (n = 99)		Coati (n = 87)		G-test value	p <
	N	PO	N	PO	N	PO		
Ungulates	19	10.6 (+)	2	1.2	1	0.7	23.21	0.001
Rabbits	13	7.2 (+)	2	1.2	1	0.7	13.34	0.01
Rodents	63	35.0 (+)	37	21.5	9	6.7 (−)	31.60	0.001
Birds	6	3.3	7	4.1	2	1.5	1.92	–
Reptiles	4	2.2	13	7.6 (+)	3	2.2	7.26	0.05
Arthropods	39	21.7 (−)	36	20.9 (−)	69	51.1 (+)	26.39	0.001
Fruit and berries	36	20.0 (−)	75	43.6 (+)	50	37.0	16.70	0.001
Trophic diversity	4.397		3.474		2.477			

N = Number of occurrences; PO = Proportion of occurrence; (+)/(−) = food eaten above/under the expected value ($p < 0.01$)

(31.2 %), and rodents (21.1 %). This could be a result of high availability of fruits and insects in spring and summer in temperate areas, as previously noted in studies on the food of coyotes (Bekoff 1977) and gray foxes (Samuel and Nelson 1982).

The main foods of coyotes were rodents (Table 1), particularly cotton rats *(Sigmodon fulviventer, S. leucotis),* representing 85 % of rodents identified. Other rodents found in coyote faeces included 8 occurrences of white-footed mice (*Peromyscus* sp.), 2 of wood rats (*Neotoma* sp.) and 1 of pocket gophers *(Thomomys umbrinus).* Arthropods (mainly Coleoptera and Orthoptera) were the second most frequently used food, followed by fruits (81 % of the occurrences were manzanita berries), wild ungulates (6 occurrences of white-tailed deer, *Odocoileus virginianus,* including 2 fawns; 1 of peccary, *Dicotyles*

tajacu), livestock (mainly pigs; probably carrion) and leporids (10 occurrences of cottontails, *Sylvilagus floridanus*, 3 of jackrabbits, *Lepus* sp.). Bird and reptiles were relatively unimportant items.

Rodents also are the major food of coyotes in other regions (e.g. BOND 1939; BOWYER et al. 1983). However, other investigators have reported leporids, deer, carrion, poultry, or fruit to be most important (MURIE 1951; BEKOFF 1982). Although consumed by coyotes (YOUNG 1951), insects are rarely a major part of the diet. Mammals were of lesser importance in the diet of La Michilía coyotes than for coyotes in other areas (BEKOFF 1977).

The major food item of gray foxes on our study area was fruit, manzanita berries comprising 96 % of the fruit occurrences. Other important items were arthropods (mainly Coleoptera), rodents (8 occurrences of white-footed mice, 6 of cotton rats, 2 of wood rats, 1 of chipmunks, *Eutamias bulleri*) and reptiles (7 lizards and 6 snakes). Birds, carrion (deer remains) and cottontails were found in lesser amounts (Table 1).

The diet of the gray fox in La Michilía is relatively similar to other studies (SAMUEL and NELSON 1982), with the exception of the low incidence of cottontails in our sample and the relatively high number of occurrences of reptiles. Usually mammals, arthropods and fruit constitute the bulk of the gray fox diet.

The coati in La Michilía mainly fed on arthropods (Table 1). From 244 individuals identified to order, 87 % were large beetles, 3.7 % grasshoppers and 3.3 % wasps. Pseudoscorpions and spiders were also found. Fruits ranked 2nd and were predominated by manzanita berries. Unidentified rodents were found in 10 % of the faeces, reptiles, birds, carrion (deer) and cottontails seem to be unimportant foods. Some categories that occurred in trace amounts in the faeces, i.e., beetle larvae, fleshy fruit and other food items consisting of soft tissue, may have been underestimated in our analysis.

These results agree with those of other studies. Insects and other invertebrates of the litter layer and a wide variety of fruit usually make up the bulk of coati foods, both in the tropics (KAUFMANN 1962) and in the drier and colder regions of the southwestern United States (KAUFMANN et al. 1976).

The feeding behaviour of coyotes, gray foxes, and coatis has been described as opportunistic (CHAPMAN and FELDHAMMER 1982), with availability playing a major role in prey selection. However, a comparison of diets of 3 predators allows for the analysis of species-specific differences in prey type preference, prey size, and trophic-niche breadth. Coyotes ate mammals more frequently, gray foxes consumed more fruits and reptiles, and coatis relied more upon arthropods and fruit (Table 1). The diet of gray foxes appears intermediate between those of coyotes and coatis. The trophic diversity and the size of the major prey were largest in the coyote, intermediate in the gray fox, and smallest in the coati. Thus, the largest predator took a greater size variety, as found by ROSENZWEIG (1966), but the gray fox (whose average weight in North America is about 3.5 kg; SAMUEL and NELSON 1982) took larger prey than the coati (average weight 4 to 6 kg; KAUFMANN 1982). Dietary overlap was similar for the pairs coyote-gray fox (B = 0.832) and gray fox-coati (B = 0.837) and less between the pair coyote-coati (B = 0.695).

Because abundance of potential prey must be similar for the 3 predator species, some of the detected differences in prey use may reflect differences in feeding ecology. Greater usage of carrion, deer and probably rabbits by coyotes than by the other species may be related to their larger size and wider range of movements. In the study area, cotton rats were common in the open habitats used by coyotes in the night (SERVÍN, pers. comm.). The 2 other predator species are typically found in wooded habitats (SAMUEL and NELSON 1982; KAUFMANN 1982) and rodents composed a smaller proportion of their diets. The higher importance of rodents and the larger prey size in the diet of the gray fox in relation to the coati possibly reflect different foraging strategies: the gray fox would have a greater hunting ability, while the coati collects foods from the litter layer (KAUFMANN 1962).

Acknowledgements

We gratefully acknowledge the assistance in the field of Don Federico and R. R. Estrella. The study was supported by an agreement between the Spanish CSIC and the Mexican CONACYT, coordinated by J. Castroviejo, Spain, and G. Halffter, México, A. P. Clevenger, E. Ezcurra, J. G. MacCracken and P. J. Polechla reviewed the manuscript. J. Servin gave us unpublished data. U. Breitenmoser translated the German summary. E. Collado and N. Bustamante also helped.

Zusammenfassung

Vergleich der Ernährungsweise von drei Carnivoren in der Westlichen Sierra Madre, Mexiko

Im Sommer 1981 und Frühling 1982 wurden Nahrungswahl und -verteilung von Kojote *(Canis latrans)*, Graufuchs *(Urocyon cinereoargenteus)* und Weißrüssel-Nasenbär *(Nasua narica)* in der westlichen Sierra Madre (Mexiko) untersucht. Die drei Arten waren zwar Generalisten, aber die Kojoten ernährten sich hauptsächlich von Nagetieren, die Graufüchse von Früchten und die Nasenbären von Arthropoden. Trophische Diversität und mittlere Beutegröße waren beim Kojoten am größten, beim Graufuchs intermediär und beim Nasenbär am kleinsten. Da das Nahrungsangebot für alle drei Arten gleich war, scheinen die Unterschiede Abweichungen im Nahrungserwerb und in der Ökologie widerzuspiegeln.

Literature

Bekoff, M. (1977): *Canis latrans.* Mammalian Species **79,** 1–9.
— (1982): Coyote *(Canis latrans).* In: Wild Mammals of North America. Ed. by J. E. Chapman and G. A. Feldhammer. Baltimore: John Hopkins Univ. Press, pp. 447–459.
Bond, R. M. (1939): Coyote food habits on the Lava Beds National Monument. J. Wildl. Manage. **3,** 180–198.
Bowyer, R. T.; McKenna, S. A.; Shea, M. E. (1983): Seasonal changes in coyote food habits as determined by fecal analysis. Am. Midl. Nat. **109,** 266–273.
Chapman, J. E.; Feldhammer, G. A. (1982): Wild Mammals of North America. Baltimore: John Hopkins Univ. Press.
Gallina, S. (1981): Forest ecosystems of northwestern México. In: Deer biology, habitat requierements and management in western North America. Ed. by Folliot, P. F., and Gallina, S. México: Instituto de Ecología, pp. 25–56.
Erlinge, S. (1968): Food studies on captive otters *(Lutra lutra).* Oikos **19,** 259–270.
Kaufmann, J. H. (1962): Ecology and social behavior of the coati, *Nasua narica,* on Barro Colorado Island, Panama. Univ. California Publ. Zool. **60,** 95–222.
— (1982): Raccoon and Allies (*Procyon lotor* and Allies). In: Wild Mammals of North America. Ed. by J. E. Chapman and G. A. Feldhammer. Baltimore: John Hopkins Univ. Press, pp. 567–585.
Kaufmann, J. H.; Lanning, D. V.; Poole, S. E. (1976): Current status and distribution of the coati in the United States. J. Mammalogy **57,** 621–637.
Lafon, A. (1983): Composición de la dieta del coyote. Nota técnica. FS-02. México: Cifonor-Inif.
Levins, R. (1968): Evolution in Changing Environments. Monogr. Pop. Biol. Princeton: Princeton Univ. Press.
Murie, A. (1951): Coyote food habits on a Southwestern Cattle Range. J. Mammalogy **32,** 291–295.
— (1974): A field guide to animal tracks. 2nd ed. Boston: Houghton Mifflin.
Pérez-Gutiérrez. C.; Fierro, L. C.; Peña, J. M.; Treviño, J. (1981): Determinación de la dieta del coyote *(Canis latrans)* a través del año en la región central de Chihuahua. Pastizales **12,** 5–6.
Pianka, E. R. (1973): The estructure of lizard communities. Ann. Rev. Ecol. Syst. **4,** 53–74.
Rosenzweig, M. L. (1966): Community structure in sympatric carnivora. J. Mammalogy **47,** 602–612.
Samuel D. E.; Nelson, B. B. (1982): Foxes (*Vulpes vulpes* and Allies). In: Wild Mammals of North America. Ed. by J. E. Chapman and G. A. Feldhammer. Baltimore: John Hopkins Univ. Press, pp. 475–490.
Sokal, R. R.; Rohlf, F. J. (1981): Biometry. San Francisco: W. H. Freeman.
Trapp, G. R.; Hallberg, D. L. (1975): Ecology of the gray fox *(Urocyon cinereoargenteus)*: a review. In: The wild canids. Ed. by M. W. Fox. New York: van Reinhold, pp. 164–178.
Young, S. P. (1951): Park I. Its history, life habits, economic status and control. In: The clever coyote. Ed. by S. P. Young and H. T. Jackson. Washington D.C.: Wildl. Manage. Inst., pp. 1–226.

Authors' addresses: Dr. Miguel Delibes, Dr. Fernando Hiraldo, Estación Biológica de Doñana, CSIC, Apartado 1056, E-41 080 Sevilla, Spain; Biol. Lucina Hernández, Instituto de Ecología, Apartado 263, Suc. B, 35 070 Gómez Palacio, Durango, México

Z. Säugetierkunde 54 (1989) 111–122

ISSN 0044-3468

Zu Funktionen des Duftdrüsenmarkierens beim Warzenschwein *(Phacochoerus aethiopicus)*

Von R. Radke und C. Niemitz

Arbeitsgruppe Humanbiologie, Freie Universität Berlin

Eingang des Ms. 4. 9. 1987

Abstract

Contribution to the Functions of Scent Marking Behaviour in the Warthog (Phacochoerus aethiopicus)

Scent marking activities of free ranging warthogs *(Phacochoerus aethiopicus)* were studied in the Masai Mara National Reserve, Kenya. In addition to ad lib.-sampling focal animals were followed continuously and marking events, their social context and the spatial distribution of marks were recorded. Marking frequencies of females increase in peripheral regions of their home ranges, while marking of males correlates more with their social activities. Males mark frequently in fights, and especially during the rut their marking activity increases drastically. They regularly mark the sleeping dens of matriarchal sounders, and cover the urine of estrous females with their own urine.

Einleitung

Die Suiden werden nach ihrer Lebensweise und Anatomie als stark olfaktorisch ausgerichtet betrachtet, aber bis auf Beobachtungen an *Sus scrofa* (Beuerle 1975; Meynhardt 1980, 1981, 1987) sind kaum Freilandbeobachtungen ihres Markierverhaltens erfolgt. Cumming (1975) und Estes et al. (1982) beschreiben einige Markierweisen beim Warzenschwein *(Pacochoerus aethiopicus),* aber auch hier fehlen bisher längere Beobachtungen freilebender Tiere.

Im Rahmen einer Untersuchung der sozialen Organisation des Warzenschweins zeigte sich, daß diese einzige in offenen Habitaten vorkommende rezente Suiden-Art eine weitgehende Übereinstimmung der Markierweisen mit dickichtbewohnenden Formen wie dem Riesenwaldschwein *(Hylochoerus meinerzhageni)* (Radke unveröff.) und dem europäischen Wildschwein *(S. scrofa)* aufweist (vgl. Beuerle 1975; Cumming 1975; Radke 1985). Mit *Ph. aethiopicus* findet sich somit eine Art, die einerseits offensichtlich noch das stammesgeschichtlich annähernd „vollständige" Markierrepertoire der Dickichtbewohner zeigt, andererseits aber eine relativ verläßliche Erfassung dieser Verhaltensweisen ermöglicht, da sie im offenen Grasland tagaktiv ist.

Material und Methode

Die Untersuchungen fanden vom Mai 1983 bis April 1984 und im April/Mai 1986 in Kenia im Masai Mara Nationalreservat statt. 1983/84 wurden die Arbeiten in einem Studiengebiet von ca. 12 km^2 durchgeführt, welches überwiegend aus *Eragrostis*-Kurzgrasland bestand. Das Areal wurde nach Warzenschweinbauten abgesucht und mit Hilfe von Luftaufnahmen kartiert. Eigene Orientierung in dem merkmalsarmen Grasland erfolgte u. a. anhand von Farbringen und Höhlennummern, die auf verstreuten *Balanites aegyptiaca*-Bäumen angebracht wurden. Lokalisierungen von Individuen oder Gruppen konnten meist nur auf 100-150 m genau vorgenommen werden, so daß eine Rasterung der Karte mit Quadraten von 200 m Seitenlänge erfolgte.

Einzeltiere konnten mit einer Fotokartei anhand spezifischer Körpermerkmale identifiziert werden. Markierereignisse wurden mit Angaben über Markierform, Ort, Kontext, Alter und Geschlecht der Tiere aufgenommen. In der Auswertung werden nur die adulten Tiere, d. h. älter als 2 Jahre,

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5402-0111 $ 02.50/0

berücksichtigt. Markierereignisse wurden bei kontinuierlichen Beobachtungen von 8 Fokustieren aufgenommen und durch Gelegenheitsbeobachtungen ergänzt. 1983/84 konnten hierbei auch die Wanderwege der Tiere dokumentiert werden. Hierzu wurde in 3-Minuten-Abständen die Belegung eines jeweiligen Planquadrates notiert, so daß die Nutzungsintensitäten der einzelnen Streifgebietflächen während des Protokollzeitraumes dargestellt werden konnten.

Wegen veränderter hochwachsender Grasgesellschaften in diesem Gebiet mußten die Arbeiten 1986 auf einem anderen Areal fortgesetzt werden, das nicht detailliert kartiert wurde, da in dieser Zeit die Beobachtung des Sexualverhaltens von Fokustieren im Vordergrund stand.

Die Arbeiten erfolgten über einen Zeitraum von ca. 1500 Feldstunden, wobei 514 Fokus-Tier-Stunden aufgenommen wurden. Insgesamt wurden dabei 664 Markierereignisse erfaßt (594 von adulten Männchen, 70 von adulten Weibchen); statistische Methoden nach Weber (1980).

Ergebnisse

Markier-Verhaltensmuster

Zum Markierverhalten des Warzenschweins wurde ein Film hergestellt (Radke 1988a), so daß auf eine detaillierte Darstellung der Bewegungsabläufe hier verzichtet werden kann und nur ein Überblick der Markierformen gegeben wird. Nach den Beschreibungen von Beuerle (1975) und Meynhardt (1980, 1981) wird das gleiche Verhaltensrepertoire mit geringen Abweichungen auch bei *S. scrofa* gefunden. Gelegenheitsbeobachtungen des Erstautors an Riesenwaldschweinen im Aberdare Nationalpark in Kenia ergaben ebenfalls die unten aufgeführten Verhaltensmuster.

Labialdrüsen-Markieren: Hierbei tritt das Tier nach einleitendem Beriechen des zu markierenden Objekts leicht vor und schiebt dabei die Hauttasche an der Basis der Eckzähne mehrmals reibend über das Objekt. Hierbei wird nach Estes et al. (1982) eine weiße, cremige Flüssigkeit aus den Drüsen gepreßt.

Wühl-Markieren: Eine Abwandlung des Markierens mit Labialdrüsen scheint eine bestimmte Form des Wühlens mit den Stoßzähnen im Boden zu sein, die sich deutlich von den üblichen Grabbewegungen unterscheidet: Während beim Graben der Kopf sagittal gehoben wird, winkelt ihn das Tier beim Wühlmarkieren stark seitlich an. Der jeweils beteiligte Eckzahn wird dabei in den Boden gebohrt. Hierbei kann Drüsensekret auf den Boden übertragen werden.

Präorbitaldrüsen-Markieren: An das Lippenmarkieren schließt sich fast immer ein Scheuern des Kopfes, besonders der Region unter den Augen, gegen das gerade markierte Substrat an. Dabei wird Sekret der Präorbitaldrüsen übertragen (Estes et al. 1982). Bei langen Markiersequenzen wechseln die Tiere auch zwischen beiden Drüsenfeldern mehrmals ab. In einigen Fällen war im Feld eine klare Trennung des Markierens mit Labial- und Präorbitaldrüsen nicht möglich; wir fassen daher beide im folgenden als „Kopfdrüsenmarkieren" zusammen.

Scharren: Beim „Scharr-Markieren" werden die Vorderläufe alternierend im Stand vor den Körper gesetzt, die Hufe flach gegen den Boden gedrückt und nach hinten gezogen. Nach Cumming (pers.Mitt.) konnte beim Warzenschwein keine Karpaldrüse nachgewiesen werden, so daß durch das Scharren möglicherweise Sekrete von Interdigitaldrüsen übertragen werden. Da eine Markierfunktion noch nicht definitiv erwiesen ist, wird die Verhaltensweise hier vorläufig als „Scharren" bezeichnet.

Harn-Markieren: Harn-Markieren wurde nur bei Männchen sicher beobachtet. Hierbei werden wahrscheinlich auch Sekrete der Präputialdrüse abgegeben. Häufig ist das stoßartige Harnspritzen (im Gegensatz zur sonst üblichen gleichmäßigen Harnabgabe) von Scharren begleitet. Nach bisherigen Beobachtungen scheinen Weibchen ihren Harn nicht gezielt an bestimmten Stellen abzusetzen. Das Weibchen W15 harnte jedoch einmal auf den von ihr mehrmals aufgesuchten und gefressenen Mageninhalt eines toten Gnus. W13, W20 und W23 wurden zwar bei der Harnabgabe unmittelbar neben von ihnen inspizierten

Höhlen beobachtet; dabei gaben die Weibchen aber jedesmal größere Mengen Harn kontinuierlich ab, so daß ein normales Urinieren vorlag.

Markierfrequenzen

Für einen geschlechtsspezifischen saisonalen Vergleich der Markierfrequenzen wurden die Markierereignisse aus Gelegenheitsbeobachtungen in den 8 Beobachtungsperioden vom September 1983 bis April 1984 auf je 100 „Feldstunden" bezogen (224 Ereignisse bei Männchen, 21 bei Weibchen, s. Abb. 1). Hieraus lassen sich also nur Aussagen über die relativen Häufigkeiten des Markierens der Geschlechter ableiten, wobei Beobachtungen an Weibchen tendenziell stärker repräsentiert sind, da immer mehr Weibchen als Männchen im Gelände angetroffen wurden. Trotzdem wurden in jeder ausgewerteten Beobachtungsperiode häufiger Männchen als Weibchen beim Markieren gesehen. Auch bei den Fokustieren waren die Frequenzen der Männchen um ein Mehrfaches größer als die der Weibchen (Tab. 1). Besonders auffällig ist die hohe Markierfrequenz der Männchen während der Paarungszeit (Abb. 1).

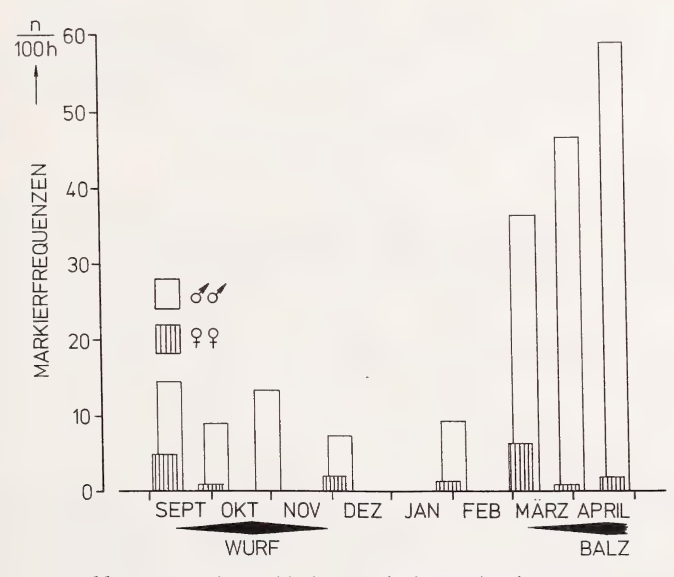


Abb. 1. Saisonale geschlechtsspezifische Markierfrequenzen

Tabelle 1. **Markierfrequenzen bei Fokustieren**

Tier	Zeitraum (Std)	Markierungen (n)	n/100 Std	Bemerkungen
W13	83,2	11	13,2	–
W15	47,4	2	4,2	Werbung
W23	42,0	1	2,4	nach Wurf
W23	82,2	18	21,9	–
W24	14,5	7	28,6	eingewandert
M7	53,8	34	63,2	Werbung
M40	147,3	101	68,6	Werbung
M43	12,1	11	90,9	Werbung
M49	31,9	24	75,2	Werbung

Da insgesamt relativ wenig Markierbeobachtungen von Weibchen vorliegen, sind nur vorläufige Aussagen über eventuelle saisonale Einflüsse möglich. Während der Brunst scheint es zu keiner Veränderung der Markieraktivität von Weibchen zu kommen, aber in der Wurfzeit markierten sie noch seltener als sonst: W23 markierte z. B. in den ersten 3 Wochen nach der Geburt ihrer Jungen in 42 Stunden nur einmal, während in den folgenden Monaten ihre Markierfrequenz fast 10mal so hoch war (vgl. Tab. 1).

Markierformen und ihr Verhaltenskontext

Weibchen markieren fast ausschließlich mit ihren Kopfdrüsen (65 von 70 Ereignissen), während sie Wühlmarkieren und Scharren nur sehr selten im agonistischen Kontext zeigten (s. Tab. 2). Männchen markieren dagegen mit Sekreten der Drüsen am Kopf, mit Harn – bzw. Präputialsekret – sowie durch Wühl- und Scharrsequenzen (Tab. 3).

Tabelle 2. **Markierform und -kontext bei Weibchen**

Form	Kontext					gesamt
	Komfort	Werbung	Kampf	HI*)	Sonstige	
Kopfdrüsen	26	2	–	13	24	65
Scharren	–	–	3	–	–	3
Wühlen	–	–	2	–	–	2
Harn	keine Markierfunktion anzunehmen					

*) Höhleninspektion

Tabelle 3. **Markierform und -kontext bei Männchen**

Form	Kontext					gesamt
	Komfort	Werbung	Kampf	HI*)	Sonstige	
Kopfdrüsen	32	32	–	127	104	295
Scharren	1	33	29	37	11	111
Wühlen	–	2	25	8	2	37
Harn	–	128	1	11	11	151

*) Höhleninspektion
G = 462; f = 12; $p < 0{,}001$, d. h. Markierform und -kontext sind signifikant voneinander abhängig.

Als Kontext wurden folgende Situationen unterschieden: „Komfort“: Markieren unmittelbar vor oder nach Scheuersequenzen; „Werbung“: Markieren unmittelbar vor, bei oder nach Werbeverhalten; „Kampf“: Markieren unmittelbar vor, bei oder nach einer Kampfsequenz; „Höhleninspektion“: Markieren unmittelbar bei einer Höhle; „Sonstige“: Markieren bei den Wanderungen oder beim Grasen. Markierform und -kontext sind bei Männchen nicht unabhängig (Tab. 3); bestimmte Markierformen treten in einigen Handlungszusammenhängen signifikant häufiger auf, als es der statistischen Erwartung entsprochen hätte (G = 462, f = 12, $p < 0{,}001$). Harn-Markieren ist z. B. meistens in eindeutig sexuellem Zusammenhang zu bemerken, während Wühl- und Scharrsequenzen besonders oft im agonistischen Kontext auftreten: In nahezu allen Auseinandersetzungen, bei denen markiert wurde, wühlte und/oder scharrte mindestens einer der Kontrahenten.

Für einen Vergleich der geschlechtsspezifischen Markieraktivitäten in den verschiedenen Handlungszusammenhängen erscheint es nicht sinnvoll, alle Markierereignisse zu berücksichtigen. Wie oben aufgeführt, fanden sich keine Hinweise für eine Markierinten-

tion bei der Harnabgabe von Weibchen, und außerdem zeigten Weibchen sehr selten ritualisierte Kämpfe mit Markiersequenzen, wie sie bei Männchen regelmäßig zu beobachten sind (Radke 1985, 1988b). In Tab. 4 sind daher Harn-Scharrsequenzen und Markierereignisse im Kampfkontext nicht aufgeführt, da hierdurch von vornherein die Markierformen von Männchen in einigen Handlungszusammenhängen überrepräsentiert würden. Die verbleibenden 399 Markierereignisse zeigen trotzdem einen signifikanten Zusammenhang zwischen Geschlecht, Markierfrequenz und Kontext (chi-Quadrat = 46,8, f = 3, $p < 0{,}001$).

Tabelle 4. **Markierfrequenz und -kontext**

	Markierereignisse bei		
Kontext	Männchen	Weibchen	gesamt
Komfort	33	26	59
Werbung	34	2	36
Höhleninspektion	161	13	174
Sonstige	106	24	130

(ohne Berücksichtigung von Kämpfen und Harn/Scharrsequenzen)
chi-Quadrat = 46,8; f = 3; $p < 0{,}001$, d. h. Geschlecht und Markierfrequenz in den verschiedenen Handlungszusammenhängen sind signifikant abhängig.

Markierfunktionen

Da beim Markierverhalten der Männchen mehrere soziale Aspekte überlagert sind, spiegelt die räumliche Anordnung ihrer Marken kaum territoriale Aspekte wider. Die räumliche Verteilung von Marken im Streifgebiet einzelner Tiere ist daher eher nach den Beobachtungen an Weibchen zu beurteilen.

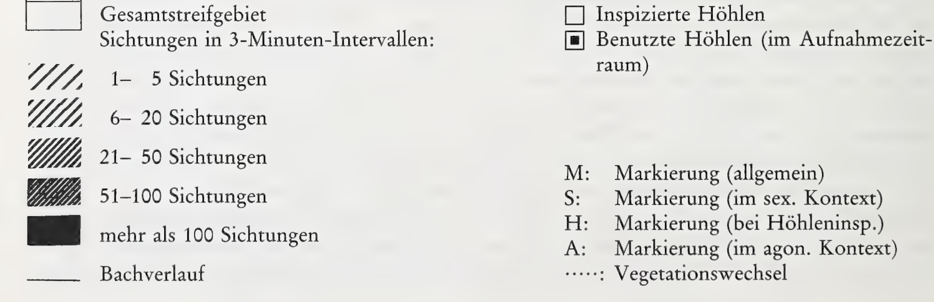
Warzenschweine sind standorttreu; sie besitzen aber keine Territorien, weder im Sinne von exklusiven, verteidigten noch von anders monopolisierten Gebieten. Eine Territorialmarkierung findet bei ihnen somit nicht statt, und wir verwenden hier den Begriff „Orientierungsmarkieren". Dabei bleibt offen, ob auch Informationen an fremde Tiere übermittelt werden, oder nur eine „Eigenorientierung" vorliegt. Markieren von Weibchen im Kontext „Sonstige" dürfte größtenteils der Orientierung der Tiere zuzurechnen sein. Die ausgedehnten Verfolgungen der Weibchen W13 und W23 zeigten hierfür klare Hinweise. In Abb. 2 sind die Planquadrate, in denen W23 im Verlaufe der Studie 1983/84 jemals angetroffen wurde, weiß dargestellt, womit das Streifgebiet des Tieres größtenteils erfaßt sein dürfte. Die schraffierten Quadrate geben die Häufigkeit der Lokalisierungen auf den entsprechenden Flächen in 3minütigen Abständen bei Dauerbeobachtungen wieder. Angegeben sind ferner die benutzten und inspizierten Höhlen sowie die Markierereignisse für die einzelnen Quadrate im protokollierten Zeitraum.

Bei Weibchen findet sich eine auffällige Häufung des Markierens in peripheren Teilen der Streifgebiete (Abb. 2). Das Weibchen W23 zeigte an den Tagen nach der Geburt ihrer Jungen weiterhin ihre üblichen Tageswanderungen; ihr genutztes Gebiet war aber deutlich kleiner und entsprach etwa ihrem zentralen Streifgebiet. An 8 protokollierten Tagen markierte sie jetzt nur einmal. Dies geschah ca. 1,5 km von der Wurfhöhle entfernt. Bei den 9 Tagesbeobachtungen mit älteren Jungen markierte sie dagegen 18mal (vgl. Tab. 1).

Unabhängig vom Kontext wurden Markierungen bei Höhlen, Suhlen und im freien Grasland unterschieden. Die 65 Markierungen von Weibchen ohne Kampfkontext verteilten sich wie folgt: 19mal bei Höhlen, 13mal bei Suhlen, 33mal im Grasland. Bei der Bewertung dieser Verteilung ist aber zu berücksichtigen, daß leicht zu markierende, reich

strukturierte Objekte wie abgestorbene Büsche besonders häufig an Höhlen vorkamen (Anlage der Bauten meist durch Erdferkel auf Termitensuche). Außerdem waren Weibchen durch ihre regelmäßigen Höhleninspektionen häufig in deren Nähe. Die Markierun-

Abb. 2. Streifgebietnutzung und Markierereignisse bei W23 – Beobachtungsdauer: 9 Tage



Gesamtstreifgebiet
Sichtungen in 3-Minuten-Intervallen:
1– 5 Sichtungen
6– 20 Sichtungen
21– 50 Sichtungen
51–100 Sichtungen
mehr als 100 Sichtungen
Bachverlauf

Inspizierte Höhlen
Benutzte Höhlen (im Aufnahmezeitraum)

M: Markierung (allgemein)
S: Markierung (im sex. Kontext)
H: Markierung (bei Höhleninsp.)
A: Markierung (im agon. Kontext)
·····: Vegetationswechsel

gen in der Nähe von Suhlen kamen immer im Zusammenhang mit Scheuersequenzen vor, hierbei wurde also eher ein Scheuerobjekt als die Umgebung einer Suhle markiert. Obwohl rund 50 % der Marken an räumlich eng begrenzten, sozial wichtigen Orten abgesetzt

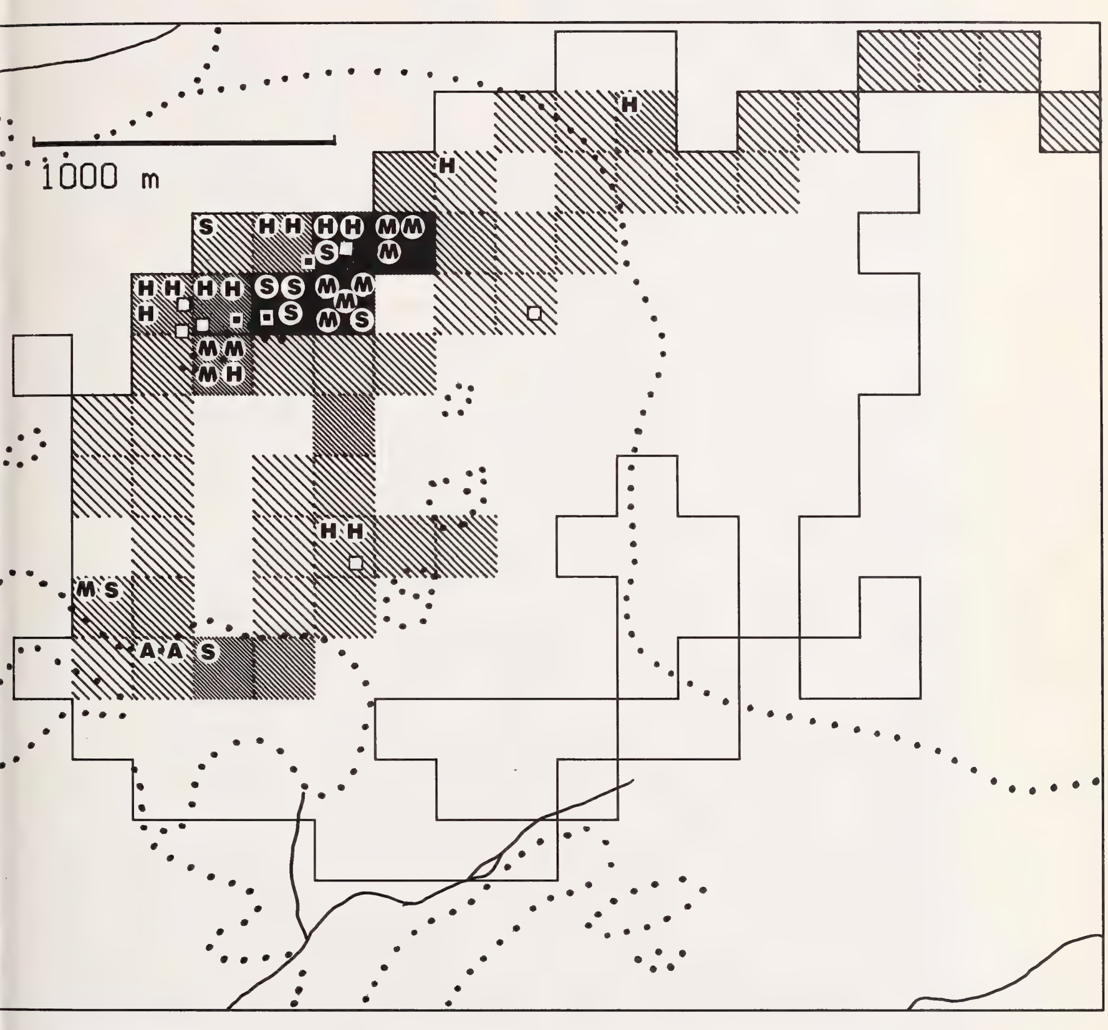


Abb. 3. Streifgebietnutzung und Markierereignisse bei M7 – Beobachtungsdauer: 5 Tage

Gesamtstreifgebiet
Sichtungen in 3-Minuten-Intervallen:
1– 5 Sichtungen
6– 20 Sichtungen
21– 50 Sichtungen
51–100 Sichtungen
mehr als 100 Sichtungen
Bachverlauf

Inspizierte Höhlen
Benutzte Höhlen (im Aufnahmezeitraum)

M: Markierung (allgemein)
S: Markierung (im sex. Kontext)
H: Markierung (bei Höhleninsp.)
A: Markierung (im agon. Kontext)
·····: Vegetationswechsel

wurden, läßt sich hieraus also nicht mit Gewißheit auf ein gezieltes, häufigeres Markieren an diesen Stellen schließen.

Bei Kämpfen markierten Weibchen 5mal; sie zeigten dabei Wühl-Markieren und Scharren. Das Markieren im Kontext „Werbung" (s. Tab. 1) besagt nach den eingangs gegebenen Kriterien nur, daß ein zeitlicher Zusammenhang mit einer Werbesequenz bestand; ein kausaler sexueller Zusammenhang ist dadurch nicht zwingend. Die Paarungsaktivitäten scheinen sich nicht in einer Veränderung der Markierfrequenz der Weibchen auszudrücken (vgl. Abb. 1).

Während bei Weibchen das Markieren mit Kopfdrüsen wahrscheinlich überwiegend der Eigenorientierung im weiteren Sinne dient, sind bei Männchen den Duftmarken aus diesen Drüsen weitere Funktionen zuzuschreiben. Allein aus den unterschiedlichen Häufigkeiten des Kopfdrüsenmarkierens der Geschlechter läßt sich ableiten, daß die hohe Markierfrequenz der Männchen nur zum Zweck der Orientierung nicht notwendig ist.

Das Weibchen W15 wurde 5 Tage vom Keiler M7 verfolgt. An allen Tagen zeigte M7 Werbeverhalten, und an 3 Tagen kam es zu jeweils einer Kopulation. Die Abb. 3 zeigt die Aufenthaltsschwerpunkte des Keilers und die Markierereignisse an den zugrundegelegten 5 Tagen (Schlüssel wie zu Abb. 2). Während W15 nur zweimal und jeweils in Randgebieten markierte, sind die 35 Marken von M7 räumlich weiter verstreut und eher nach den Aufenthaltsschwerpunkten verteilt. Auffällig ist ferner die hohe Markierfrequenz von M7 bei Höhlen. Hierbei war es immer W15, welche die Höhlen aufsuchte und teilweise minutenlang inspizierte, während M7 oft nur flüchtig die Eingänge prüfte, aber dann ausgiebig Sekrete der Präorbital- und Labialdrüsen absetzte (in Abb. 3 sind daher nicht alle von M7 aufgesuchten Bauten als „inspiziert" ausgedruckt).

Bei morgendlichen und abendlichen Beobachtungen eines ausgedehnten Höhlenkomplexes fiel in der Paarungszeit immer wieder auf, daß Männchen, die diese Höhlen nur sehr selten zum Übernachten benutzten, die Löcher geradezu patroullierten. Hierbei waren die Männchen offenbar sexuell gestimmt, denn sie scharrten und harnmarkierten dabei relativ oft – Markierweisen, die typisch für den Werbekontext sind (s. Tab. 3). Wurden Weibchen in einer Höhle angetroffen, wartete der Keiler meist, bis die Gruppe den Bau verließ und prüfte dann durch Geruchskontrolle den Östruszustand der Weibchen. 1986 konnte in 2 Fällen beobachtet werden, daß Männchen die Fährten von Gruppen an Höhlen aufnahmen und sie bis zu den Weibchen verfolgten. Regelmäßig benutzte Höhlen sind für Keiler offensichtlich relativ verläßliche Treffpunkte mit potentiellen Geschlechtspartnern.

In keinem Fall war eine abweisende Wirkung von Duftmarken festzustellen. Bestimmte Äste an einigen Höhlen wurden in kurzen Abständen von verschiedenen Männchen markiert. Der Geruch wirkte zumindest auf junge Tiere und Weibchen eher anziehend: Mehrmals wurden Weibchen und Juvenile beim Beriechen von Marken älterer Männchen beobachtet, wobei anschließend eigene Marken darüber gesetzt werden konnten, oder die Tiere die markierte Stelle zum Scheuern benutzten. Mehrmals reagierten auch jüngere Männchen auf von alten Keilern frisch abgesetzte Marken, indem sie diese berochen oder übermarkierten. Eine Reaktion von alten Männchen auf die Marken von jüngeren Tieren konnte nicht festgestellt werden, obwohl mehrmals starke Keiler neben jüngeren, markierenden Männchen standen.

Harnmarkieren ist regelmäßig in sexuellem Kontext zu bemerken. Männchen übersprühen Harn von Weibchen während der Brunft fast immer mit ihrem eigenen Harn; zusätzlich wird gelegentlich an der Stelle gescharrt. Die Harn- und Scharrbeobachtungen im Kontext „Sonstige" (vgl. Tab. 3) sind wahrscheinlich auf ältere Harnstellen von Weibchen zurückzuführen. Bei einer Gelegenheit harnte und scharrte ein Männchen z. B. an einer Stelle, an der vorher ein Männchen bei einem Weibchen gesehen worden war. Ein anderes Mal wurde der Liegeplatz eines östrischen Weibchens von einem begleitenden Männchen übersprüht.

Diskussion

In der Literatur wurde die räumliche Verteilung von Marken vor allem unter territorialen Aspekten untersucht, wobei eine Funktion des Markierens zur Erzeugung einer geruchlich vertrauten Umgebung angenommen wird. Es zeigen sich jedoch keine generellen Zusammenhänge von Markierverhalten und Besitz eines Territoriums (Zusammenfassung für afrikanische Ungulaten in Leuthold 1977, s. a. Walther 1984). Die aufgeführte Markenanordnung beim Warzenschwein ist ebenfalls nicht unter territorialen Gesichtspunkten zu sehen: Die periphere Verteilung dient sicher nicht als „Grenzmarkierung". Näherliegend dürfte ein Vertrautmachen mit einer fremden Umgebung durch eigene Geruchsmarken sein. Dies war recht deutlich bei W24 zu erkennen, das im August 1983 in das Studiengebiet einwanderte. In der für dieses Tier noch „neuen" Umgebung markierte es an 3 Tagen in ca. 25 Stunden 7mal – die höchste beobachtete Markierfrequenz bei einem Weibchen (Tab. 1).

Der Abfall der Markierhäufigkeit während der Wurfzeit wäre nach den o. g. Kriterien auf den Aufenthalt der Weibchen in vertrauten Gebieten in der Nähe ihrer Wurfhöhlen zu erklären. Ferner können Marken auch Freßfeinden Hinweise auf die Anwesenheit potentieller Beute geben. Die Jungen, welche in den ersten Wochen für bis zu 5 Stunden alleine in der Wurfhöhle zurückgelassen werden, sind auch in den Höhlen durch eine Reihe von Predatoren gefährdet. Weibchen sollten jetzt also „vorsichtiger" im Anzeigen ihrer Gegenwart sein. Dies gilt in geringerem Maße auch für den Rest des Jahres, wenn die Jungen die Mutter begleiten, während die Männchen derartige „Rücksichten" nicht nehmen müssen.

Die Funktion des Markierens zum „Inventarisieren" zeigte sich sehr deutlich an folgendem Verhalten: Bei der Kartierung wurden Höhlen mit einem Holzpfahl versehen, der die Höhlennummer und einen weißen stark riechenden Lackstreifen trug. Diese Pfähle lösten anfänglich Fluchtreaktionen aus und wurden erst nach ausgiebigem Markieren nach 7–10 Tagen „akzeptiert". Danach benutzten die Schweine sie gelegentlich als Markierstellen, wie sie es auch mit Büschen in Höhlennähe taten.

Soziale Bedeutungen des Markierens lassen sich eher aus den Beobachtungen von Männchen ableiten, wie sich aus dem deutlichen Anstieg ihrer Markierfrequenzen während der Paarungszeit ergibt. Erschwert wird die Diskussion durch den Umstand, daß olfaktorische Reize auf mehreren Ebenen wirken und – je nach Rezipient – völlig verschiedene Funktionen haben können. So können die Marken für das markierende Tier ein „Geruchsfeld" bilden, das in Streßsituationen bestärkend wirkt (vgl. Diskussionen bei Eisenberg und Kleimann 1972; Johnson 1973). Ralls (1971) schließt aus Gefangenschaftsbeobachtungen am Maxwellducker *(Cephalophus maxwelli)* und an verschiedenen Kleinsäugern, daß eine hohe Markierfrequenz Ausdruck von Dominanz oder Angriffsbereitschaft sei. Bei Warzenschweinen ist eine derartige Korrelation nicht zu erkennen: junge, aber geschlechtsreife Männchen im Alter von ca. 30 Monaten markierten an Höhlen ebenso ausgiebig wie alte Keiler. Mit Kopfdrüsen wurde meist in Abwesenheit anderer Tiere markiert; keine Verhaltensreaktion auf Geruchsmarken läßt auf Dominanz- oder Subordinationsverhalten schließen. Auch bei Auseinandersetzungen ist eine Wirkung der Duftmarken auf den Kontrahenten bisher nicht zu erkennen: Die Männchen scharrten und wühlten mit Vorderläufen und Schnauzen den Boden, wobei sie gelegentlich das für intensives Riechen stereotype Kopfschütteln zeigten. Ein Beriechen der Markierspuren des Gegenübers konnte dabei jedoch nie beobachtet werden (vgl. Radke 1988b).

Walther (1984) gibt einen sehr umfassenden Überblick ähnlicher Verhaltensweisen im agonistischen Kontext bei verschiedenen Huftiergruppen, wonach Scharr- und Wühlsequenzen weit verbreitet sind ('object aggression'). Diese „Erregungshandlungen" werden meist sehr formstarr ausgeführt und als weitgehend visuell wirksame Imponier- bzw. Drohsignale aufgefaßt (Zusammenfassungen in Leuthold 1977 und Walther 1984). Es erscheint in diesem Zusammenhang von Bedeutung, daß dieses Verhalten schon bei den als

relativ ursprünglich eingeordneten Suiden vorkommt (vgl. auch Beuerle 1975). Nach den hier vorliegenden Befunden spielt bei ihnen die olfaktorische Komponente möglicherweise noch die wesentliche Rolle, während bei den moderneren Huftieren diese Bewegungsweisen zunehmend ritualisiert und visualisiert wurden. Da Kämpfe unter Warzenschweinkeilern oft nur durch Imponierauftritte (inklusive Markiersequenzen) entschieden werden (Radke 1985, 1988b), sind auch bei Warzenschweinen neben der geruchlichen „Selbstbestärkung" visuelle Imponierwirkungen der Markierbewegungen anzunehmen. Scharren und Wühl-Markieren sind im Kampfkontext besonders häufig, weil hierbei jederzeit Angriffe eines Gegners abgefangen werden können. Das übliche Markieren mit den Kopfdrüsen erfordert hingegen geeignete Objekte in der Nähe, sowie ein Abwenden vom Gegner.

Bei Hausschweinen wirkten die Sekrete der Präputialdrüse sowie Steroide der Submaxillardrüsen im Test als Attraktans (Hafez und Signoret 1969; Mykytowycz (1977). Meynhard (1987) fand zwar bei Tests mit dem künstlichen Eberpheromon „Suidor" keine anziehende Wirkung auf freilebende Wildschweinsauen, aber nach Mykytowycz (1977) waren die untersuchten Steroide nur bei Körpertemperaturen wirksam, was bei Meynhardts Tests nicht gewährleistet war. Warzenschwein-Weibchen wurden mehrmals beim Aufsuchen und Beriechen frisch mit Präorbital- und Labialdrüsensekret markierter Stellen beobachtet, so daß diese Marken möglicherweise auch beim Warzenschwein als Attraktans dienen. Die Schlafhöhlen der Weibchen sind besonders wichtige Treffpunkte der Geschlechter. Einzelne Weibchen-Gruppen benutzten bei 36 Übernachtungen bis zu 17 verschiedene Höhlen, d. h. sie haben Wahlmöglichkeiten zwischen mehreren Quartieren, so daß östrische Weibchen durchaus oft von Männchen aufgesuchte Bauten bevorzugen könnten.

Wie weiter oben aufgeführt, wäre eine intensive Markieraktivität von Weibchen zur Anlockung von Männchen mit Risiken durch Freßfeinde behaftet. Tatsächlich fanden sich keine Hinweise für erhöhte Markierfrequenzen der Weibchen während der Paarungszeit. Genau betrachtet kann auch die Markieraktivität der Männchen Predatoren auf besonders oft benutzte Bauten hinweisen, d. h. die Strategien der Geschlechter widersprechen einander auf diesem Gebiet.

Meynhardt (1980, pers. Mitt.) sah zu Beinn der Rauschzeit auch bei Wildschweinsauen eine erhöhte Markieraktivität; quantitative Vergleiche zu den Markierfrequenzen der Keiler fehlen aber bisher. Beuerle (1975) fand nur bei Keilern intensives Markieren während der Paarungszeit, wobei es sich allerdings um gegatterte Tiere handelte. Jones (1978) konnte beim Buschschwein *(Potamochoerus porcus)* nur an dem untersuchten Männchen eine Labialdrüse nachweisen, während bei einem Weibchen keine derartige Drüse gefunden wurde, so daß auch bei *P. porcus*-Männchen ein komplexeres Markiersystem als bei den Weibchen vorliegt. Bei Hirschen der Gattung *Odocoileus* fanden sich 7- bis 8fache Markierfrequenzen der Männchen (Müller-Schwarze 1977). Hier handelt es sich möglicherweise um ein allgemeines Phänomen polygyner oder promiskuitiver Arten (vgl. auch weitere Beispiele bei Johnson 1973).

Olfaktorische Reize wirken außerdem noch auf einer dritten Ebene. Wie durch die Hausschweinzucht bekannt ist, können sie bei Weibchen den Eintritt der Geschlechtsreife, den Östrusbeginn und die Einnahme der Kopulationsstellung (Lordosis) beeinflussen (Hafez und Signoret 1969; Brooks und Cole 1970; Überblick in Mykytowycz 1977). Eberpheromone werden in der Schweinezucht regelmäßig zur Weibchen-Stimulierung benutzt, und Meynhardt (pers. Mitt.) konnte durch Besprühen von freilebenden Wildschweinen mit dem Pheromon "Suidor" verläßlich den Östrusbeginn auslösen. Die während der Paarungszeit rapide ansteigende Markierfrequenz der Männchen spielt möglicherweise somit auch eine Rolle bei der Induzierung des Östrus sowie bei der Verbesserung der Synchronisierung der Brunst.

Warzenschweine sind promiskuitiv mit einer intensiven sexuellen Konkurrenz unter

den Männchen. Unter derartigen Umständen wird es für einen Keiler wichtig, potentielle Rivalen im unklaren über den Östruszustand des jeweils begleiteten Weibchens zu lassen. Der Zustand des Weibchens wird bei Säugern allgemein mittels Harnkontrollen durch die Männchen bestimmt (s. z. B. ESTES 1972). Warzenschweinkeiler überdecken durch ihren eigenen Harn den weiblichen Urin und erschweren damit möglicherweise einem nachfolgenden Rivalen die Analyse. Hinweise für einen „Besitzanspruch" auf das Weibchen oder eine allgemein abschreckende Wirkung der Männchen-Harnmarken fanden sich auch hier nicht. Paarungspartner waren vielmehr regelmäßig von weiteren Männchen begleitet, die durch direkte Angriffe des jeweils stärksten Männchens vertrieben oder auf Abstand gehalten wurden (RADKE, unveröff.). Das Übermarkieren des Weibchen-Harns wäre demzufolge als Anpassung zur Reduzierung des Verteidigungsaufwandes für Paarungspartner aufzufassen, indem Herausforderern der aktuelle „Paarungswert" des umstrittenen Weibchens verschleiert wird. Wie bei der Betrachtung des Markierens im agonistischen Kontext könnte das Harnmarkieren der Warzenschweine ebenfalls als stammesgeschichtlich alte Verhaltensweise im ursprünglichen Handlungszusammenhang gesehen werden. In den wesentlich stärker strukturierten Sozialsystemen moderner Huftiere, wo es im direkten Paarungszusammenhang selten zu Auseinandersetzungen unter paarungsberechtigten Männchen kommt, stellt dementsprechend Harn-Markieren im sexuellen Kontext nur noch ein Verhaltensrudiment dar, bzw. es ist auf andere Bereiche wie die Territorialmarkierung übertragen (vgl. WALTHER 1984).

Danksagung

Die kenianischen Behörden gaben die Forschungsgenehmigung und stellten Arbeits- und Unterkunftsräume im Masai Mara Nationalreservat; der Deutsche Akademische Austauschdienst und die Ständige Kommission für Forschung und wissenschaftlichen Nachwuchs (FNK) der Freien Universität Berlin unterstützten die Arbeiten durch ein Stipendium bzw. einen Sachmittelzuschuß; Prof. H. KLINGEL regte die Untersuchung an, stellte großzügig Teile seiner Ausrüstung zur Verfügung und begleitete die Arbeiten durch fachliche Anregungen; Dr. W. PANDIKOW und Fam. D. BURCHARD gewährten dem Erstautor in Nairobi freundliche Beherbergung; M. BITZAN und U. SAUTER erstellten die Abbildungen. Ihnen allen sei herzlich gedankt.

Zusammenfassung

Markierereignisse bei freilebenden Warzenschweinen wurden im Masai Mara Nationalreservat in Kenia mit Angaben zu Markierform, Kontext, Ort und Geschlecht der Tiere aufgenommen. Von Fokustieren wurden zusätzlich die Wanderwege registriert und die Markierereignisse den verschiedenen Bereichen der Streifgebiete zugeordnet. Markiert wurde besonders in peripheren Teilen der Streifgebiete bzw. an fremdartigen Gegenständen. Da die Streifgebiete verschiedener Tiere einander vollständig überlappten, scheint es sich hier nicht um eine Grenzmarkierung, sondern um das Vertrautmachen einer Umgebung bzw. um eine Inventarisierung zu handeln. Markiert wird außerdem regelmäßig bei Kämpfen, wobei die Marken des Gegners nicht beachtet werden. Die Markierfrequenz der Männchen steigt in der Paarungszeit auf ein Mehrfaches an. Vornehmlich in der Nähe von Weibchen-Schlafhöhlen markieren Männchen besonders häufig, wobei derartige Marken als Attraktans für östrische Weibchen dienen dürften. Männchen überdecken Harn von östrischen Weibchen regelmäßig mit ihrem eigenen Harn und maskieren auf diese Weise die olfaktorische Information des weiblichen Urins.

Literatur

BEUERLE, W. (1975): Freilanduntersuchung zum Kampf- und Sexualverhalten des Europäischen Wildschweines *(Sus scrofa)*. Z. Tierpsych. **39**, 211–258.

BROOKS, P. H.; COLE, D. J. A. (1970): The effect of the presence of a boar on the attainment of puberty in gilts. J. Reprod. Fert. **23**, 435–440.

CUMMING, D. H. M. (1975): A field study of the ecology and behaviour of warthog. Mus. Mem. **7**, Salisbury.

EISENBERG, J. F.; KLEIMANN, D. G. (1972): Olfactory communication in mammals. Ann. Rev. Ecol. Systems **3**, 1–32.

Estes, R. D. (1972): The role of the vomeronasal organ in mammalian reproduction. Mammalia **36,** 315–341.
Estes, R. D.; Cumming, D. H. M.; Hearn, G. W. (1982): New facial glands in domestic pig and warthog. J. Mammalogy **63,** 618–624.
Hafez, E. S. E.; Signoret, J. P. (1969): The behaviour of swine. In: The behaviour of domestic animals. Ed. by E. S. E. Hafez. London: Balliere, Tindall & Cox. 349–390.
Johnson, R. P. (1973): Scent marking in mammals. Anim. behav. **21,** 521–535.
Jones, M. A. (1978): A scent marking gland in the bushpig, *Potamochoerus porcus*. Arnoldia **30,** 1–4.
Leuthold, W. (1977): African ungulates: A comparative review of their ethology and behavioural ecology. Berlin Heidelberg, New York: Springer.
Meynhardt, H. (1980): Untersuchungen zur akustischen, olfaktorischen und visuellen Kommunikation des Europäischen Wildschweins *(S. scrofa)*. Beitr. Forstwissensch. **2,** 72–82.
— (1981): Schwarzwild-Report. Melsungen: Neumann-Neudamm.
— (1987): Verhaltensbiologische Untersuchungen an Europäischen Wildschweinen sowie verwilderten Hausschweinen und Schlußfolgerungen für die praktische Schweineproduktion. Diss. Karl-Marx-Universität, Leipzig.
Müller-Schwarze, D. (1977): Complex mammalian behavior and pheromone bioassay in the field. In: Chemical signals in vertebrates. Ed. by D. Müller-Schwarze and M. M. Mozell. New York, London: Plenum Press. 413–433.
Mykytowycz, R. (1977): Olfaction in relation to reproduction in domestic animals. In: Chemical signals in vertebrates. Ed. by D. Müller-Schwarze and M. M. Mozell. New York, London: Plenum Press. 207–224.
Radke, R. (1985): Zur Ökologie und Ethologie des Warzenschweins *(P. aethiopicus)*. Diplomarbeit Freie Universität Berlin.
— (1988a): D 1659 Duftmarkieren beim Warzenschwein *(P. aethiopicus)*. IWF Göttingen.
— (1988b): D 1658 Kampfverhalten beim Warzenschwein *(P. aethiopicus)*. IWF Göttingen.
Ralls, K. (1971): Mammalian scent marking. Science **171,** 443–449.
Walther, F. (1984): Communication and expression in hoofed mammals. Bloomington: Indiana University Press.
Weber, E. (1980): Grundriß der biologischen Statistik. Jena: Gustav Fischer.

Anschrift der Verfasser: Dipl. Biol. Reinhard Radke und Prof. Dr. Carsten Niemitz, Freie Universität Berlin, FB 23, WE 1, Fabeckstr. 15, D-1000 Berlin 33

Z. Säugetierkunde 54 (1989) 123–124

ISSN 0044-3468

WISSENSCHAFTLICHE KURZMITTEILUNG

Patterns of association among *Peromyscus leucopus* using artificial nest boxes during the fall

By J. W. Popp

Receipt of Ms. 24. 5. 1988

After the breeding season, white-footed mice *(Peromyscus leucopus)* begin to nest communally at day refuge sites (Madison et al. 1984; Wolff and Durr 1986). The onset of communal nesting is generally preceeded by a move from arboreal nest sites to nest sites below-ground or low in trees (Madison et al. 1984). Although mean group sizes and sex composition of groups have been reported (Wolff and Durr 1986), it is not known whether lasting associations exist between individuals in communal nests. I investigated this aspect of *Peromyscus leucopus* social organization during the fall through the use of artificial nest boxes.

The study site was located in a mature, upland forest dominated by sugar maple *(Acer saccharum)*, white ash *(Fraxinus americana)*, American beech *(Fagus grandifolia)*, hophornbeam *(Ostrya virginiana)*, and shagbark hickory *(Carya ovata)*. Artificial nest boxes (12 × 12 × 12 cm with 2.5 cm opening on one side) were placed 1 to 2 m high on the nearest tree to a grid point in a 9 by 9 grid with 10 m between grid points (0.64 ha area). Nest boxes were placed at the site the week of 18 October 1987 and were first checked the week of 1 November 1987. Wood chips and sawdust was provided in each box for bedding. Nest boxes were checked between 0800 and 1200 CST, one to two times a week (12 times in all), until the last week in December. At the end of December, use of the nest boxes as day refuges ceased as the mice presumably moved to below ground sites. Each time the nest boxes were checked the identity of each individual was noted. On first capture, each individual was toe-clipped, sexed, and aged, based on pelage coloration, as either an adult or subadult. Mice captured at least twice were considered to be resident on the study grid.

A total of 23 mice were captured 72 times. Eighteen mice (nine adults, nine subadults) were resident on the study grid. The most common groupings in order of occurrence were: adult male and female (10 times); lone adult male (9); lone adult female (7); lone subadult male (6); adult male, adult female and mixed sex subadult group (3); adult female with mixed sex subadult group (3); and mixed sex subadult group (2). In addition, the following groups were each captured once; lone subadult female, adult male with subadult female, and two subadult males. Mean group size was 1.95 (SD = 1.18, range 1–5).

The nine resident adults were captured 43 times. Based on their patterns of association adults could be divided into two groups; those that rarely associated with other adults and those that were frequently associated with another adult. Five of the adults (three males, two females) were typically found either alone or with subadults. In only one case was an adult male-female group found. In contrast, the other four adults were typically caught as male-female pairs. One male and female were found seven times each and in each instance they were together (twice they were also associated with subadults). Another pair was trapped together five times. These two individuals were never found with other adults, although the female was found alone once.

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5402-0123 $ 02.50/0

The nine resident subadults (five males, four females) were captured only 24 times. Because of the low recapture rate, only four subadults were recaptured two or more times in communal nests, so it was difficult to determine if subadults maintained long-term associations. There were two cases of a subadult being found twice with the same adult female. In another case, two subadults (a male and female) were found together on three occasions. These associations may represent mother-offspring or sibling relationships (WOLFF and DURR 1986).

Of the 49 recaptures, 13 occurred in the same nest box as the original one, 26 occurred in adjacent boxes, and 9 recaptures were made in boxes two grid points away. Only one recapture occurred more than two grid points away from the original capture site. Captures were made at 21 different nest boxes. These boxes were used by a mean of 1.95 different individuals (SD = 1.2, range 1–5). When only nest boxes at which residents were captured are considered, a mean of 2.3 individuals used each box.

It has been suggested that communal nesting among rodents during the winter may be advantageous for conserving heat by huddling, gaining access to limited nest sites, or for avoiding predation (WEST and DUBLIN 1984). None of these potential advantages, however, require long-term associations between individuals. The results of this study suggest that some, but not all, adults maintain an association with an individual of the opposite sex in terms of their use of day refuges. Further research is needed to determine if these pairings are simply non-breeding season associations or if they also represent breeding pairs. *Peromyscus leucopus* is reportedly promiscuous (WOLFF and LUNDY 1985), so it is unlikely that these pairings represent strictly monogamous relationships.

Acknowledgements

I thank JAMES REINARTZ and LINDA BUNKFELDT-POPP for their help throughout this project, especially for sharing their mouse handling expertise. This is contribution no. 109 of the University of Wisconsin-Milwaukee Field Station.

References

MADISON, D. M.; HILL, J. P.; BLEASON, P. E. (1984): Seasonality in the nestling behavior of *Peromyscus leucopus*. Am. Midl. Nat. **112**, 201–204.

WEST, S. D.; DUBLIN, H. T. (1984): Behavioral strategies of small mammals under winter conditions. In: Winter ecology of small mammals. Ed by J. F. MERRITT. Spec. Publ. Carnegie Mus. Nat. Hist. **10**, 1–380.

WOLFF, J. O.; DURR, D. S. (1986): Winter nesting behavior of *Peromyscus leucopus* and *Peromyscus maniculatus*. J. Mammalogy **67**, 409–412.

WOLFF, J. O.; LUNDY, K. I. (1985): Intra-familial dispersal patterns in white-footed mice, *Peromyscus leucopus*. Behav. Ecol. Sociobiol. **17**, 831–834.

Author's address: Dr. JAMES W. POPP, Field Station, University of Wisconsin-Milwaukee, Saukville, WI 53080, USA

BUCHBESPRECHUNGEN

GRZIMEK, B. (Hrsg.): **Grzimeks Enzyklopädie Säugetiere – Band 3.** München: Kindler Verlag 1988. 648 S., zahlreiche Abb., Lexikon-Großformat, Leinenausgabe. DM 148,–. ISBN 3-463-42003-1. Luxusausgabe (Halbleder) DM 198,–, ISBN 3-463-42103-8

Von der auf fünf Bände konzipierten „Grzimeks Enzyklopädie Säugetiere" liegt nunmehr Band 3 vor, der die Nagetiere und von den Raubtieren Marder, Bären, Schleichkatzen, Hyänen und einen Teil der Katzen behandelt. Der Aufbau dieses Werkes gleicht dem der anderen Bände, so daß es mit einem Hinweis auf eine andere Besprechung in dieser Zeitschrift sein Bewenden haben kann (s. KRUSKA in Vol. 53, S. 266). 23 Fachkollegen haben sich der Mühe unterzogen, viele biologische, ökologische und ethologische Daten zusammenzutragen, wobei je nach Kenntnisstand (Zoobeobachtungen, Freilandstudien, Laborhaltung, wirtschaftliche Bedeutung) und „Attraktivität" den einzelnen Arten ein unterschiedlich breiter Raum eingeräumt wird. Bei der Vielzahl der Autoren, aber auch bei dem unterschiedlichen Bekanntheitsgrad, dessen sich die verschiedenen Arten erfreuen, konnte es nicht ausbleiben, daß straff gehaltene Darstellungen mit breiter angelegten abwechseln, wobei auch einzelne oder gelegentliche Freilandbeobachtungen in die Ausführungen einfließen. Das liegt in der Natur der Sache und wiederholt sich in den anderen Bänden.

In den Text sind zahlreiche Farbfotos eingeflochten, die rasch über Aussehen, Körpergröße und Färbung der jeweiligen Art informieren. Informativ sind auch die Verbreitungskarten, die rasche Orientierung über das Vorkommen vieler Arten gewährleisten. Die Behauptung, der Band lebe von seinen Farbbildern, würde der Zielsetzung der Enzyklopädie und seiner Bedeutung als moderne Informationsquelle nicht gerecht. Dennoch muß es erlaubt sein, auf die hervorragende Qualität der ganzseitigen Fotos hinzuweisen, die als Momentaufnahme oft besondere Lebenssituationen kennzeichnen. Manche Aufnahmen sind auch ganz einfach nur brillant. Die Fülle der besprochenen Arten verbietet es, auf Einzelheiten einzugehen. Für die Sachlichkeit der Ausführungen verbürgen sich anerkannte Säugetierforscher. Manche Unausgewogenheit der Darstellung war wohl nicht zu vermeiden. So werden der Familie der interessanten Dipodidae, die in 27 Arten Eurasien und Nordafrika bewohnen, nur 3½ Seiten gewidmet, dem Biber indessen acht.

Grzimeks Tierleben hat mit Grzimeks Tierenzyklopädie einen Nachfolger gefunden, der als unentbehrliches Nachschlagewerk in jede Fachbibliothek gehört. Das Werk empfiehlt sich nicht nur für interessierte Laien, Schüler, Studenten und Fachlehrer als gewinnbringende Lektüre, auch der auf Spezialgebieten tätige Mammaloge dürfte zwecks rascher Information zu diesen Bänden greifen. Der Verlag und seine Mitarbeiter haben eine herausgeberische Leistung vollbracht, die Anerkennung verdient.

H. REICHSTEIN, Kiel

SEDLAG, U.: **Wie leben Säugetiere?** Leipzig, Jena, Berlin: Urania-Verlag 1988. 248 S., 55 Farbfotos, zahlreiche Randzeichnungen. DM 32,–. ISBN 3-332-00190-6

Die vorliegende Biologie der Säugetiere wendet sich an einen interessierten Leserkreis in allgemein verständlicher Form und setzt nur voraus „was jeder über Bau und Funktion des eigenen Körpers weiß, zudem manches andere aus dem in der Schule vermittelten Grundwissen". „Ausgangspunkt ist das lebende Tier als Glied seiner Lebensgemeinschaft und Produkt seiner Umwelt. Körperbau und physiologische Funktionen werden meist nur soweit besprochen, wie es zum Verständnis bestimmter Leistungen oder auch ihrer Grenzen erforderlich erscheint."

Nach diesem Motto werden Anpassungen an Klimafaktoren, die Bewegungs- und Ernährungsweisen, Tages- und Jahreslauf, die Demökologie, die Variabilität der wichtigsten Sinne, Signale und Intelligenz und die Beziehungen zu Artgenossen und Artfremden behandelt. Im Vordergrund steht die Verknüpfung spezieller Eigenschaften aus den verschiedensten Lebensbereichen, z. B. von Ernährungsweise, Sozialstruktur und Verbreitung oder die Einpassung der Fortpflanzung in den Jahreslauf. Der Autor hat einen sehr umfangreichen Stoff und zahlreiche jüngste Befunde zusammengetragen und es verstanden, das Wesentliche einfach, oft in anschaulichen Bildern und vielfach mit Hinweis auf alltäglich erscheinende Beobachtungen an Haus- und Zootieren zu schildern.

Mancher Gedanke ist neu, eigenständig und regt zu experimenteller Nachprüfung an. Die farbigen Fotos, aber auch die Zeichnungen sind von guter bis ausgezeichneter Qualität. Zu vielem, so zur Zahnzahl, zur Verbreitung verschiedener Ernährungstypen bei den Fledermäusen, über die Belastung der Mutter durch Trächtigkeit und Laktation oder Kopfwaffen und ihren Gebrauch gibt es tabellarische Übersichten, vergleichende Graphiken oder Zeichnungen. Gemessen am reichen Inhalt finden sich kaum sachliche Fehler: In der Zahnformel des Rindes (S. 44) sind die Vorderzähne versehentlich nach oben geraten, S. 53 ist von Blinddarmkot der Waldspitzmaus die Rede, obwohl diese, wie die Abb. des Darmtrakts S. 69 auch richtig zeigt, nicht die Spur eines Blinddarms besitzt.

Die Abbildungslegenden sind öfter zu knapp geraten. So ist die über den Auskühlungseffekt des Windes (S. 11) schwer verständlich, weil darin Wärme und Temperatur vermengt sind. Die Erklärung

zu den Füßen von vier Paarzehern (S. 25) findet man ganz knapp auf S. 24 oben. Bei den Backenzahn-Aufsichten (S. 47) fehlt ein Hinweis über die Orientierung.

Schließlich enthält das Buch eine Fülle von Angaben, die selbst manchem Fachzoologen erstaunlich erscheinen oder neu sind, und denen er gern nachgehen würde. So wird über Beobachtungen von Kämpfen zwischen Narwal-Männchen berichtet oder darüber, daß Koalas das für Beuteltiere hohe Geburtsgewicht von 4 g haben. Hier ist es bedauerlich, daß jeglicher Hinweis auf die Literatur fehlt. Ein zweiseitiges Verzeichnis gibt zwar weiterführende Literatur an, doch darauf nimmt der Text keinen Bezug. Gewiß hätte ein umfassendes Zitatengerüst die Lesbarkeit stark beeinträchtigt, aber gegenüber der etwas lückenhaften systematischen Übersicht (Eismeerringelrobbe, Kurznasenflughund, Amerikanisches Mausohr und Ratte z. B. kommen nur im laufenden Text vor) wären ein ausführliches Literaturverzeichnis und Hinweis im Text doch hilfreich gewesen, besonders weil das ingesamt sehr ansprechende Buch gewiß geeignet ist, der Säugetierkunde neue Freunde zu gewinnen.

J. Niethammer, Bonn

Kämpfe, L.; Kittel, R.; Klapperstück, J.: **Leitfaden der Anatomie der Wirbeltiere.** 5., überarb. Aufl. Stuttgart: Gustav Fischer 1987. 309 S., 205 Abb., 4 Tab. DM 38,–. ISBN 3-437-20389-4 (Linzenausgabe)

Acht Jahre nach Erscheinen der 4. Aufl. liegt dieser bekannte kurzgefaßte Leitfaden über die Anatomie der Wirbeltiere nun in einer überarbeiteten 5. Aufl. vor. Die bewährte inhaltliche Gliederung der vorangegangenen Aufl. wurde beibehalten, so daß im Anschluß an einen Überblick über das System der Chordaten und Darstellungen zur Kennzeichnung gruppenspezifischer Abläufe von Individualentwicklungen folgende Organsysteme aus vergleichender Sicht abgehandelt werden: Bewegungsapparat; Coelom; Gastro-Pulmonalsystem; Zirkulationssystem; Urogenitalsystem; endokrine Organe; Nervensystem; Sinnesorgane; Haut. Ein kurzer Abschnitt über die Stammesgeschichte schließt sich an.

Gegenüber der 4. Aufl. ist eine Einführung neu, in der auf Bewertungsprobleme von Homologien und Konvergenzen in Kürze eingegangen wird. Darüber hinaus sind an mehreren Stellen des Textes Änderungen, Ergänzungen oder Umstellungen vorgenommen worden (z. B. Somiten, Knochen, Knorpel, innersekretorische Organe, Stammesgeschichte etc.). In Zusammenhang damit erscheinen 8 neue Abbildungen, andere der vorangegangenen Aufl. sind umgezeichnet worden oder weggefallen. Grundsätzlich wird auch in dieser modernisierten Fassung sehr viel Wissen in Kürze und in einem besonders preisgünstigen Buch geboten. Eine weite Verbreitung, vor allem unter Studierenden ist daher zu erwarten. Gerade im Hinblick auf diese Vermutung erscheinen jedoch einige Anmerkungen erforderlich. Nach Ansicht des Rezensenten liegt es in der besonderen Verantwortung von Lehrbuch-Autoren, überlieferte und neue wissenschaftliche Sachverhalte dem Entwicklungsstand entsprechend in klarer Sprache darzulegen. Nicht nur in bezug auf den Kenntnisstand, sondern auch in sprachlicher Formulierung, präziser Beschreibung und einem gewählten Ausdruck sollte der Wissende dem Lernenden als Vorbild gegenübertreten. In dieser Hinsicht sind jedoch bedauerlicherweise selbst in der vorliegenden überarbeiteten Aufl. immer noch zweifelhafte und mißverständliche Formulierungen sowie fehlerhafte Aussagen erhalten geblieben, neue kommen hinzu. Besonders störend erscheinen weder zwingende noch schlüssige, simplifizierte Darstellungen von Kausalzusammenhängen, die gedanklich überholte Vorstellungen zum evolutiven Wandel der Organismen erneut erwecken könnten. Folgende zwanglose Auswahl von Zitaten mag dieses belegen:

„Da nun das Wassermilieu fehlte, mußten Vorkehrungen getroffen werden, die eine Austrocknung der Eier verhindern. ... Dieser Schutz allein reicht jedoch nicht aus, so daß die Eier laufend befeuchtet werden müssen." (S. 29). „Zwischen den Binnenzellen tritt ein Spaltraum auf, der die Veranlassung zur Bildung einer Blastocyste gibt." (S. 32). „Das mit Nährstoffen und Sauerstoff beladene mütterliche Blut wird über die Placenta dem Keimling zugeführt, ohne daß es zu einem Übertritt von Blutkörperchen kommt. ... Der Transport der verschiedenartigsten Stoffe kann nicht schrankenlos vor sich gehen, da viele Eiweißstoffe individualspezifisch sind, ... Diese Scheidewände einschließlich der Gefäßwandungen sind einem schnellen Stoffübertritt ... hinderlich, deshalb besteht die Tendenz, die Anzahl der Trennwände zu reduzieren." (S. 34). „Die Wirbelkörper (Centra) bestehen zumindest bei niederen Vertebraten aus vier Bogenstücken, ..." (S. 39). „Der Bau der Vorderextremität vieler Mammalia ist weitgehend durch ihr Laufverhalten beeinflußt." (S. 57).

Ferner bleiben in manchen Abb. Fehler erhalten (z. B. Bezeichnung von Schädelknochen, Pons bei Reptilien- und Vogelgehirn), zum Teil werden fehlerhafte Abb. sogar im Text korrigiert (S. 54). Die Unterschrift zu Abb. 139 lautet: „Schemata über das Verhalten der ♂ Urogenitalsysteme."

Diesem gut konzipierten Leitfaden ist für zukünftige Auflagen eine gründliche Überarbeitung des Textes und der Abb. dringlich zu empfehlen.

D. Kruska, Kiel

SANS-COMA, V.; MAS-COMA, S.; GOSÁLBEZ, J. (eds.): **Mamiferos y Helmintos.** Barcelona: Ketres Editora. 1987. 388 S.; Abb., Tab. 6000 pts. ISBN 84-85256-70-0

Der Sammelband ist Prof. Dr. HERMANN KAHMANN aus München zu seinem 81. Geburtstag am 9. Oktober 1987 gewidmet, der vor allem nach seiner Pensionierung in fördernden Gedankenaustausch mit jungen spanischen Säugetierkundlern trat und sich in einer Serie von Arbeiten mit der Biologie und Morphologie balearischer Gartenschläfer befaßte. Einer Würdigung des Jubilars folgen je 11 Beiträge über iberische Kleinsäuger und über Helminthen – größtenteils in Säugetieren lebende Arten. Die sorgfältig redigierten, gediegenen Beiträge sind spanisch mit englischer Zusammenfassung. Hier nur einige Bemerkungen zu den Arbeiten über Säugetiere: Zusammenfassend geben SANS-COMA et al. auf Rasterkarten die Verbreitung von Insektenfressern und Nagern in Südspanien wieder und behandeln ihre Taxonomie. Maßtabellen für Waldmaus, Haus-, Wanderratte und *Microtus duodecimcostatus* sind hier hervorzuheben. LANGE und ALCOVER liefern eine metrische Analyse für *Erinaceus algirus* von den Balearen, LOPEZ-FUSTER und VENTURA über *Sorex coronatus.* LLUCH et al. untersuchten *Talpa europaea* aus einem Höhenintervall zwischen 200 und 2000 m NN, ohne eine regelhafte Beziehung zwischen Körpergröße und Meereshöhe zu finden. SANS-COMA et al. betrachten neben der Balg- und Schädelmorphologie bei der Hausspitzmaus auch die Einpassung ihres Haarwechsels und ihrer Fortpflanzung in den Jahreslauf. ALCOVER behandelt die Verteilung rezenter und fossiler Gartenschläfer (*Eliomys*) und verwandter Arten auf den Inseln des Mittelmeers. Hausratten pflanzen sich in Südspanien von Februar bis Oktober fort und haben 1–12, im Mittel 6,7 Embryonen (ZAMGRANO et al.). *Mus spretus* ist in südspanischen Zuckerrohrkulturen im Sommer überwiegend nacht-, im Winter auch tagaktiv (VARGAS et al.).

Wer sich für die geographische Variabilität in Körperbau und biologischen Eigenschaften, aber auch für die Verbreitung kleiner Säugetiere auf der Iberischen Halbinsel interessiert, wird im vorliegenden Band eine Menge solider Angaben dazu finden.

J. NIETHAMMER, Bonn

PATTERSON, B. D.: **Studies in neotropical mammalogy.** Essays in honour of Philip Hershkovitz. Fieldiana: Zool. (NS) 39. Chicago, Illinois: Field Museum of Natural History 1987. 506 S., etwa 153 Abb., 63 Tab. $ 35.00. ISSN 0015-0754

Neben einer kurzen Biographie von PHILIP HERSHKOVITZ enthält der Band 27 Arbeiten über südamerikanische Säugetiere vor allem zur Taxonomie, aber auch über die Lebensweise. Eine ausführliche Erforschungsgeschichte von der Entdeckung Südamerikas bis 1850 hat HERSHKOVITZ selbst beigesteuert. Mit biographischen Angaben, Darstellung der Reisewege, Auszügen aus Reiseberichten und Deutungsversuchen der gesammelten Säugetiere befaßt sie sich etwa mit MARCGRAF, FERREIRA, VON SPIX, Prinz WIED, NATTERER, VON HUMBOLDT, BONPLAND, AZARA, MOLINA, TSCHUDI und DARWIN. PASCUAL und CARLINI beschreiben aus dem späteren Oligozän Patagoniens Unterkieferfragmente eines Marsupialiers mit Nagergebiß (dauerwachsende Schneide- und Backenzähne) und ordnen sie einer neuen Überfamilie Patagonioidea zu. IZOR und PINE ergänzen das Wissen über die Beutelratte *Caluromysiops irrupta* Sanborn, 1951, bieten ein Habitusfoto und eine Schädelzeichnung, Maße und Verbreitungsangaben. Eine Revision der Gattung *Artibeus* aus dem nördlichen Südamerika von HANDLEY enthält einen Bestimmungsschlüssel für die kleineren Arten und zwei Art-Neubeschreibungen: *A. amplus,* eine mit 70 mm Unterarmlänge sehr große Form, und eine linear nur gut halb so große Zwergform, *A. gnomus.* Ein reizvolles Thema ist der „Zeltbau" durch *Artibeus*- und *Uroderma*-Arten (TIMM). Gemeint ist das Benagen großer Blätter in einer Weise, daß die Teile zu zeltartigen Gebilden zusammenfallen, die diesen Fledermäusen als Tagesrastplatz dienen. PHILLIPS, NAGATO und TANDLER fanden in den sekretorischen Speicheldrüsenzellen von 15 neotropischen Fledermausarten aus vier Familien eine erstaunliche Vielfalt der elektronenoptischen Bilder der Sekretgranula bei innerartlicher Konstanz. Unter den taxonomischen Beiträgen sind Revisionen des Reisratten-Subgenus *Oligoryzomys,* der Stachelratten *(Proechimys)* und der Akodontini hervorzuheben. Als Beispiele zoogeographisch-phylogenetischer Arbeiten seien Beiträge über die Octodontiden und die südamerikanischen Caniden genannt. Für die Caniden wird ein durch Synapomorphien gestütztes Kladogramm präsentiert. Fossilfunde, von denen die ältesten aus dem Spätpliozän (grob vor etwa 2 Millionen Jahre) stammen, sind hier einbezogen.

Der Band präsentiert also eine Fülle recht bedeutender Arbeiten über Säugetiere Südamerikas, vor allem Beuteltiere, Fledermäuse und Nager, daneben auch Primaten, Cerviden, Carnivoren, die zum Teil allgemeineres Interesse beanspruchen. Druck, Papier, Wiedergabe der Abbildungen und redaktionelle Gestaltung sind ausgezeichnet. Die Sammlung von Arbeiten kann Säugetierkundlern nur uneingeschränkt und nachhaltig empfohlen werden.

J. NIETHAMMER, Bonn

Schober, W.; Grimmberger, E.: **Die Fledermäuse Europas; kennen – bestimmen – schützen.** Kosmos Naturführer. Stuttgart: Franckh'sche Verlagshandlung 1987. 224 S., DM 36,–. ISBN 3-440-05796-8

In vielen europäischen Ländern sind Fledermäuse seit mehreren Jahren zunehmend in der Diskussion, weil Ausweitungen und Intensivierung von Kulturräumen des Menschen zu erheblichen Gefährdungen von Beständen und Artenzahlen dieser Kleinsäuger geführt haben. In einigen Ländern gibt es regional bereits erhebliche Initiativen, die noch vorhandenen heimischen Arten durch besonderen Schutz zu erhalten und zu vermehren. Der vorliegende Naturführer leistet einen willkommenen Beitrag zu diesen Bemühungen.

In einem ersten Kapitel berichten die Autoren in Kürze über das Leben der Fledermäuse, deren Entdeckungsgeschichte und Bedeutung für den Menschen, besondere Anpassungen, Prinzipien der Echo-Orientierung, Sozialverhalten, Winterschlaf und Wanderungen; in einem folgenden Abschnitt über Schutzmaßnahmen und deren Erfolge. Den größten Umfang nimmt die Beschreibung der 30 in Europa heimischen Arten aus den Familien Rhinolophidae (5), Vespertilionidae (24) und Molossidae (1) ein. Diese werden nach folgendem einheitlichem Schema abgehandelt: Körpermaße, Kennzeichen, Färbungsanomalien, ähnliche Arten, Verbreitung, Biotop, Wanderungen, Fortpflanzung, Höchstalter, Jagd und Nahrung, Laute, Schutzsituation. Anschließend findet der Leser einen Bestimmungsschlüssel und vergleichende Abbildungen von Nasenaufsätzen, Ohrformen, Schwanzflughäuten und anderen Merkmalen sowie Sonagramme und tabellarische Gegenüberstellungen von biologischen und ökologischen Daten. Wichtigste Meßstrecken am Körper werden ebenfalls abgebildet.

Dieser Naturführer ist zusätzlich durch zahlreiche Farbphotos illustriert und zeigt eine ansprechende Aufmachung. Er wird sicherlich einen großen Interessenkreis finden. D. Kruska, Kiel

Fenton, M. B.; Racey, P.; Rayner, J. M. V. (eds.): **Recent Advances in the Study of Bats.** Cambridge, London, New York: Cambridge Univ. Press 1987. 470 pp. £ 50.00. ISBN 0-521-32160-3

In diesem Band wurden 21 Beiträge zusammengefaßt, die auf der 7th International Bat Research Conference/3rd European Symposium on Bat Research (19.–24. August 1985 in Aberdeen, Schottland) gehalten wurden.

Die ersten sieben Beiträge befassen sich mit verschiedenen Aspekten des Fledermausfluges: K. Padian versucht eine phylogenetische Ableitung des Fluges unter Berücksichtigung funktioneller Faktoren. Er kommt zu dem Schluß, daß sich die Chiropteren aus arborealen Gleitfliegern entwickelt haben. Den Mechanismus des Fluges analysiert J. Rayner; U. Norberg und H. Baagoe untersuchen die Bedeutung der Flügelform für Flugstil und -geschwindigkeit. Die beiden folgenden Kapiteln behandeln physiologische Aspekte des Fluges.

Einen breiten Raum nehmen Untersuchungen zur Echoortung ein. Es werden dabei sowohl neuere Verhaltensexperimente vorgestellt, als auch verschiedene neurophysiologische Arbeiten diskutiert. W. E. O'Neill gibt eine Übersicht über die Verarbeitung der zeitlichen Information im ZNS, M. Vater erläutert am Beispiel von *Rhinolophus* und *Pteronotus* die Frequenzanalyse im auditiven System, und H.-U. Schnitzler demonstriert, daß im Echo fliegender Insekten bei den CF/FM-Fledermäusen rhythmische Frequenzänderungen auftreten, die es ihnen ermöglichen, die Beuteinsekten auch in einer stark schallreflektierenden Umgebung zu detektieren.

Der dritte Abschnitt des Buches ist verschiedenen Problemen der Reproduktion gewidmet. Es werden sowohl die genetische Struktur der sozialen Gruppen analysiert (G. F. McCracken), als auch am Beispiel südamerikanischer Phyllostomatiden die Bedeutung altruistischer Verhaltensweisen aufgezeigt (G. S. Wilkinson). J. R. Speakman und P. A. Racey untersuchen die Fortpflanzung von *Plecotus auritus* unter energetischen Gesichtspunkten.

Dieses Buch bietet eine Fülle von Information über Chiropteren, wobei besonders hervorgehoben werden muß, daß in jedem Kapitel neben den aktuellen Forschungsergebnissen eine ausführliche Diskussion der Literaturdaten eingearbeitet wurde. Dadurch hebt sich das Buch positiv von den meist sehr speziellen Symposiumsbänden ab und wird für längere Zeit ein Standardwerk für den an Fledermäusen interessierten Biologen darstellen. Die gute Ausstattung rechtfertigt den relativ hohen Preis. U. Schmidt, Bonn

Subscription information for USA, Canada and Mexiko obtainable from Paul Parey Scientific Publishers/IR Unltd., 35 West 38th Street, Suite 3 W, New York, NY 10018, USA.

Erscheinungsweise und Bezugspreis 1989: 6 Hefte bilden einen Band. Jahresabonnement Inland: 318,– DM zuzüglich 13,80 DM Versandkosten, Gesamtpreis 331,80 DM einschließlich 7 % Mehrwertsteuer. Jahresabonnement Ausland: 318,– DM zuzüglich 18,– DM Versandkosten. Das Abonnement wird zum Jahresanfang berechnet und zur Zahlung fällig. Es verlängert sich stillschweigend, wenn nicht spätestens am 15. November eine Abbestellung im Verlag vorliegt. Die Zeitschrift kann bei jeder Buchhandlung oder bei der Verlagsbuchhandlung Paul Parey, Spitalerstraße 12, D-2000 Hamburg 1, bestellt werden. Die Mitglieder der „Deutschen Gesellschaft für Säugetierkunde" erhalten die Zeitschrift unberechnet im Rahmen des Mitgliedsbeitrages.

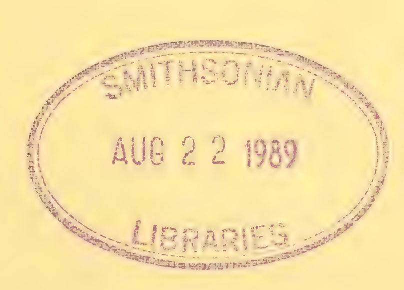
Z. Säugetierkunde 54 (1989) 2, 65–128

Vol. 54 (3), 129–192, Juni 1989 ISSN 0044-3468 C 21274 F

ZEITSCHRIFT FÜR SÄUGETIERKUNDE

INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde





Verlag Paul Parey Hamburg und Berlin

This journal is covered by Biosciences Information Service of Biological Abstracts, and by Current Contents (Series Agriculture, Biology, and Environmental Sciences) of Institute for Scientific Information

---

Die Zeitschrift für Säugetierkunde veröffentlicht Originalarbeiten und wissenschaftliche Kurzmitteilungen aus dem Gesamtgebiet der Säugetierkunde, Besprechungen der wichtigsten internationalen Literatur sowie die Bekanntmachungen der Deutschen Gesellschaft für Säugetierkunde. Verantwortlicher Schriftleiter im Sinne des Hamburgischen Pressegesetzes ist Prof. Dr. Harald Schliemann.

Zusätzlich erscheint einmal im Jahr ein Heft mit den Abstracts der Vorträge, die auf der jeweiligen Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde gehalten werden. Sie werden als Supplement dem betreffenden Jahrgang der Zeitschrift zugeordnet. Verantwortlich für ihren Inhalt sind ausschließlich die Autoren der Abstracts.

Manuskripte: Manuskriptsendungen sind zu richten an die Schriftleitung, z. Hd. Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Biologie-Zentrum, Neue Universität, Olshausenstr. 40–60, D-2300 Kiel. Für die Publikation vorgesehene Manuskripte sollen gemäß den „Redaktionellen Richtlinien" abgefaßt werden. In ihnen finden sich weitere Hinweise zur Annahme von Manuskripten, Bedingungen für die Veröffentlichung und die Drucklegung, ferner Richtlinien für die Abfassung eines Abstracts und eine Korrekturzeichentabelle. Die Richtlinien sind auf Anfrage bei der Schriftleitung und dem Verlag erhältlich.

Sonderdrucke: Anstelle einer Unkostenvergütung erhalten die Verfasser von Originalbeiträgen und Wissenschaftlichen Kurzmitteilungen 50 unberechnete Sonderdrucke. Mehrbedarf steht gegen Berechnung zur Verfügung, jedoch muß die Bestellung spätestens mit der Rücksendung der Korrekturfahnen erfolgen.

Mit einer Beilage des Verlages Paul Parey

Fortsetzung 3. Umschlagseite

© 1989 Paul Parey. Verlag: Paul Parey, Hamburg und Berlin. Anschriften: Spitalerstr. 12, D-2000 Hamburg 1; Lindenstr. 44–47, D-1000 Berlin 61. – Printed in Germany by Westholsteinische Verlagsdruckerei Boyens & Co., D-2240 Heide/Holst.

Z. Säugetierkunde 54 (1989) 129–140
© 1989 Verlag Paul Parey, Hamburg und Berlin
ISSN 0044-3468

Cytogenetics and karyosystematics of phyllotine rodents (Cricetidae, Sigmodontinae)

II. Chromosome multiformity and autosomal polymorphism in *Eligmodontia*

By M. O. Ortells, O. A. Reig, R. L. Wainberg, Graciela E. Hurtado de Catalfo, and Teresa M. L. Gentile de Fronza

Grupo de Investigación en Biología Evolutiva, Departamento de Ciencias Biológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina, and Cátedra de Biología General, Departamento de Ciencias Biológicas, Facultad de Ciencias Exactas, Universidad Nacional de La Plata, La Plata, Argentina

Receipt of Ms. 10. 9. 1987

Abstract

Studied the bone-marrow and gonadal karyotypes, and the G- and C-banding of phyllotine mice of the genus *Eligmodontia* from different localities in Argentina. Twenty-eight specimens from Chasico, southern Buenos Aires Province, and from different localities of north eastern, south eastern and central Chubut showed a karyotype of 2n = 44, FNa = 44 comprised of one pair of large metacentric, 20 pairs of much smaller telocentric autosomes and a X-Y sexual system. One out of twelve individuals from Chasico, showed a 2n = 43 Robertsonian variant of the same karyotype. Three specimens from Los Lagos, Neuquen, showed a quite different and polymorphic karyotype of 2n = 32–33, FNa = 32, consisting at the homozygous state of 14 pairs of telocentric, 1 pair of metacentric autosomes and the sexual pair. Additionally, the karyotype of 2n = 50, FNa = 48 from Peru, formerly briefly described by Pearson and Patton (1976), is illustrated and compared with the other two. The hypothesis is advocated that these three different cytotypes or chromosomal forms represent three different species. Thus, *Eligmodontia,* classically treated as a monotypic genus, is considered to be polytypic. The names *Eligmodontia typus*, and *E. puerulus* are provisionally proposed for the Buenos Aires-Chubutian, and the Peruvian cytotypes, respectively. The name to apply to the Neuquenian cytotype is discussed, but is considered unsolvable at the present state of knowledge.

Introduction

Eligmodontia is a genus of South American cricetids belonging to the phyllotine radiation (Reig 1986) which is striking because of its adaptations to life in arid biomes (Mares 1975, 1977). These long tailed and long eared mice with a long and silky fur are widespread in the southern cone of South America, from south of Peru to Tierra del Fuego.

The systematics of *Eligmodontia* is considered very simple since Hershkovitz's (1962) revision, which only recognizes a single species with two subspecies: *E. typus typus* Cuvier, 1837, and *E. typus puerulus* Philippi, 1896, from seven allegedly different species described previously. In view of the widespread distribution and diversity of habitats of *Eligmodontia* populations, one is tempted to surmise that Hershkovitz went too far in synonymizing all proposed species of this genus in just one species with two subspecies.

To test the alternative monotypic or polytypic hypotheses of species diversity in *Eligmodontia*, the karyological information can be an efficient tool. Unfortunately, chromosome information is almost nil in *Eligmodontia*. The few published data are the mention by Pearson and Patton (1976) of a karyotype of 2n = 50, FNa = 48 for *Eligmodontia typus* from southern Peru, and the preliminary account of the chromosomes of a population from Chasico that we further discuss in this paper (Hurtado de Catalfo and Wainberg 1977).

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5403-0129 $ 02.50/0

As a result of our current karyotyping of cricetids captured as a by-product of other research interests, the present authors found two extremely different karyotypes in samples of *Eligmodontia* from Argentina which differ from that reported by PEARSON and PATTON. We decided to join our results presenting the evidence gathered so far, which cogently favor the polytypic hypothesis.

Material and methods

We studied the chromosomes of 32 individuals (21 males, 11 females) from six localities in southern Argentina (Fig. 1): Pampa de Salamanca, Puerto Madryn, Paso de Indio, 28 de julio (Chubut Province); Los Lagos (Neuquen Province), and Chasicó (Buenos Aires Province). The animals were captured with Sherman live traps, and processed in our laboratories in Buenos Aires and La Plata. Skin and skull voucher specimens were deposited in the collection of Mammals of the Municipal Museum of Natural History at Mar del Plata (MMP), the Museum of Zoology, University of Wisconsin (MZW) and the Museum of La Plata (MLP).

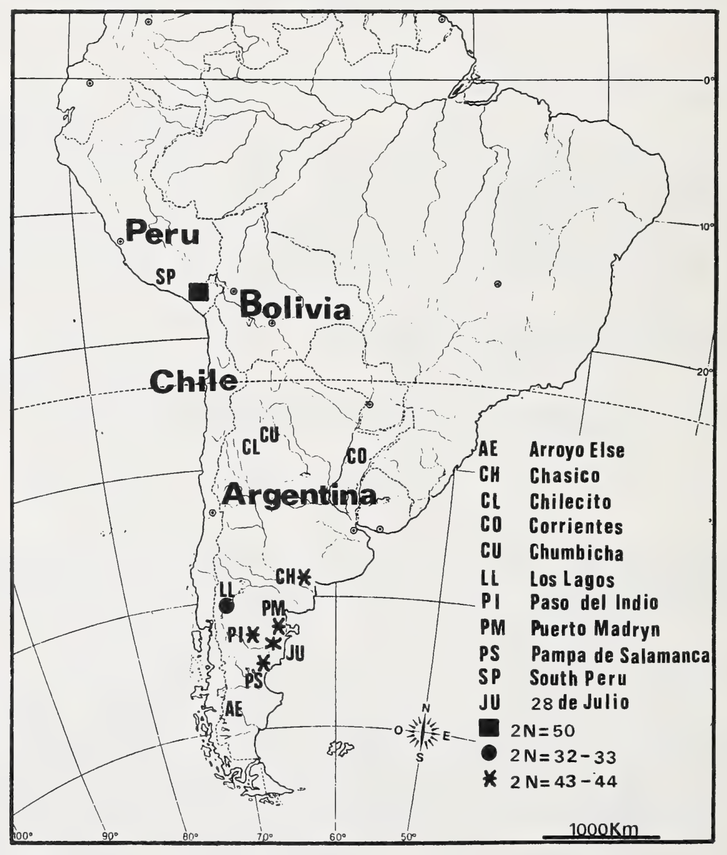


Fig. 1. Map showing where samples of *Eligmodontia* studied in this paper were collected and localities cited in the text. Diploid numbers are indicated for the former

We processed the bone marrow chromosomes following the techniques described in ROTHFELS and SIMINOVITCH (1958) and in REIG et al. (1971). G- and C-banding were obtained using the techniques of SEABRIGHT (1971) and SUMNER (1972), respectively. Male meiosis was studied in testicular direct preparations (EVANS et al. 1964). We followed LEVAN et al. (1964) for the nomencla-

ture of chromosomes according to the centromere position. Idiograms of each karyotype were constructed by measuring at least 10 enlarged metaphase prints. FNa are autosomal numbers. For the assortment of chromosomes in size classes, we called large those chromosomes measuring >9 % of the length of the female haploid complement; medium-sized those ranging from 5.5 to 9.0, small those ranging from 2 to 5.5 %, and microchromosomes those measuring <2 % of the female haploid chromosomal length.

Results

Twelve individuals from Chasico and 16 individuals from the four localities in Chubut Province showed an identical 2n = 44, FNa = 44 karyotype (Fig. 2). One female individual from Chasico showed a 2n = 43, FNa = 44 variant of the same karyotype. The animals

Table 1. **Mean values ($\bar{x}$), standard deviation (SD) and number of metaphases (N) measured of chromosomes of *Eligmodontia typus*, expressed as a percentage of the female haploid set. Arm ratio = long arm/short arm**

Chromosome	N	Total Length $\bar{x}$	Total Length SD	Arm Ratio $\bar{x}$	Arm Ratio SD
1	11	17.6	.91	1.1	.05
2	11	6.6	.26	∞	
3	11	6.0	.22	∞	
4	11	5.2	.17	∞	
5	11	4.9	.10	∞	
6	11	4.7	.11	∞	
7	11	4.4	.07	∞	
8	11	4.1	.19	∞	
9	11	3.9	.15	∞	
10	11	3.8	.11	∞	
11	11	3.7	.22	∞	
12	11	3.5	.18	∞	
13	11	3.3	.15	∞	
14	11	3.2	.13	∞	
15	11	3.0	.21	∞	
16	11	3.0	.17	∞	
17	11	2.9	.17	∞	
18	11	2.8	.11	∞	
19	11	2.6	.21	∞	
20	11	2.4	.24	∞	
21	11	1.9	.32	∞	
X	11	6.8	.57	1.30	.25
Y	11	3.5	.41	5.00	1.87

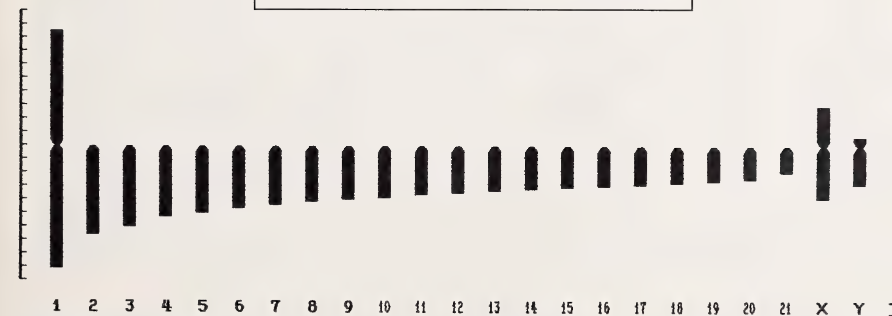


Fig. 2. Idiogram of *Eligmodontia typus*, 2n = 44, FNa = 44

from Los Lagos, Neuquen, showed a quite different karyotype: one female and one male showed a karyotype of 2n = 33, FNa = 32, and one male a 2n = 32, FNa = 32 variant.

The autosomal set of the 2n = 44 karyotype shows a pair of large (17.6 %) metacentric (r = 1.06) chromosomes followed by 20 pairs of telocentric chromosomes grading in size from medium-sized (pair 2–4), to small (pairs 5–19) and microchromosomes (pairs 20–21) (Table 1, Figs. 2 and 3). The X is a medium sized (6.5 %) metacentric, and the Y is a small (3.5 %) subtelocentric chromosome. G-bands allow us to correctly establish the homologies of all chromosomes (Fig. 4). C-banding (Fig. 5) showed a pericentromeric C-positive region on all autosomal pairs. The X chromosome also shows pericentromeric heterochromatin, but in addition two C-positive lighter bands are present in the long arm. The Y is fully C-positive. The 2n = 43 karyotype of the single female individual from Chasico (Fig. 6) differs from the above described 2n = 44 karyotype in having a medium sized odd biarmed autosome and two odd small-sized telocentric autosomes. We failed to obtain good G-banding in this individual, but chromosomal measurements allow us to infer that the short and the long arm of the odd metacentric correspond to one chromosome of autosomes pairs 5 and 18, respectively of the 2n = 44 karyotype. Thus, a Robertsonian fusion/fission translocation is here in case. 2n = 44 chromosomes are also present in the studied spermatogonial metaphases. In diakinesis and metaphase I cells we recognized 21 autosomal bivalents and the sexual bivalent. X and Y chromosomes show a meiotic end-to-end pairing. Pair I bivalent is obviously much larger than the remaining, and it usually shows three (Fig. 7) and less frequently only two chiasmata. The remaining bivalents show just one chiasma.

We have been unsuccessful in obtaining banding chromosomes in specimens from Los Lagos. As represented by one male individual, the "normal" karyotype of this form of 14 pairs of telocentric and one pair of metacentric autosomes and an X-Y sexual system (Fig. 8 and 9). There is a rather abrupt size gap between pairs 1–6 and the remaining autosomal pairs (Table 2). Pairs 1–5 are large, pair 6 medium-sized, but chromosomes of this group decrease gradually in size. Pair 7 is a medium sized metacentric. Pairs 8 to 15 are all telocentric chromosomes gently decreasing in size from medium sized to small. A clear-cut secondary constriction is evident on autosomal pairs 4 and pair 9, similar to those present in the karyotype of the Peruvian form reported by Pearson and Patton (1976) (Fig. 10). The X is a medium sized (5.8 %) telocentric, and the Y is a small metacentric chromosome.

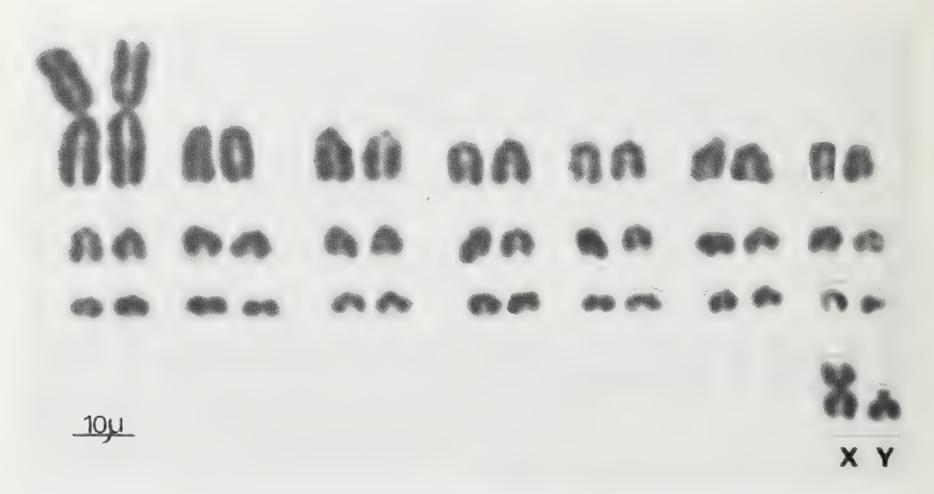


Fig. 3. Bone marrow standard Giemsa staining karyotype of *Eligmodontia typus* from Puerto Madryn, Chubut Province, Argentina, 2n = 44; FNa = 44

10μ

X Y

Fig. 4. G-banded karyotype of *Eligmodontia typus* from Puerto Madryn, Chubut Province, Argentina. 2n = 44; FNa = 44. In the rectangle, elongated first pair of autosomes of another metaphase of the same animal is included to better appreciate the G-banding pattern

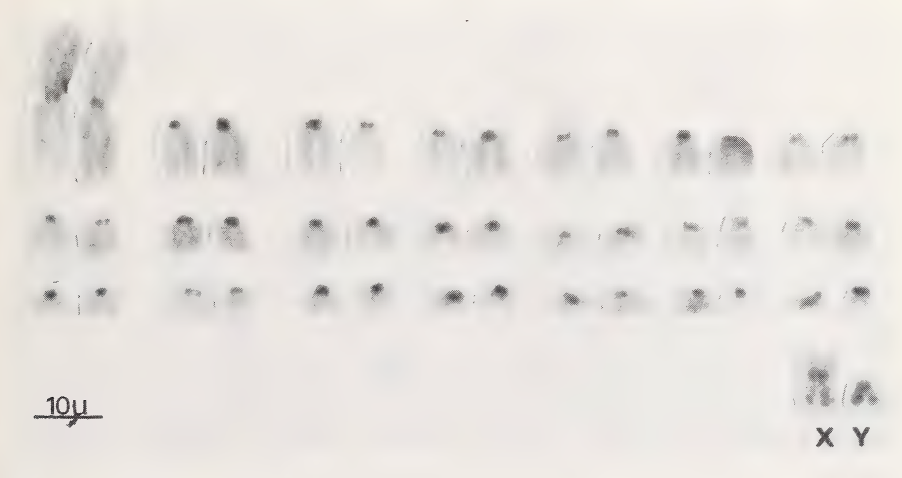


Fig. 5. C-banded karyotype of *Eligmodontia typus* from Puerto Madryn, Chubut Province, Argentina. 2n = 44; FNa = 44



Fig. 6. Bone marrow standard Giemsa staining metaphase and karyotype of the polymorphic form of *Eligmodontia typus* from Chasico, Buenos Aires Province, Argentina. 2n = 43; FNa = 44. The chromosomes involved in the postulated Robertsonian rearrangement are represented in the upper right corner

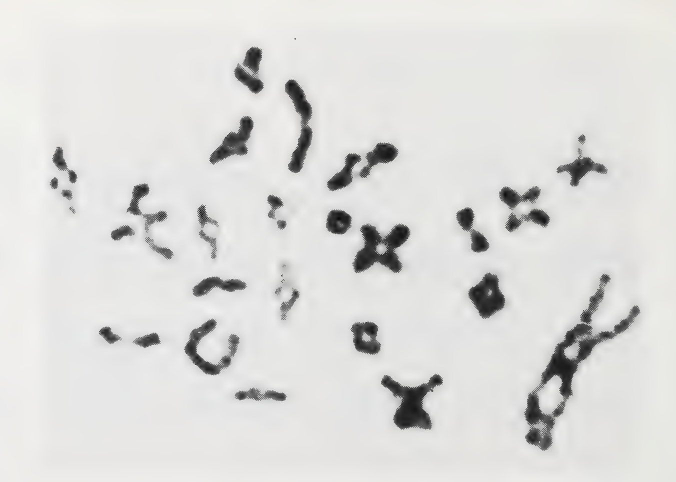


Fig. 7. Diacinesis of *Eligmodontia typus* from Chasico Buenos Aires Province, Argentina, showing the usual three chiasma configuration in pair one. 2n = 44; FNa = 44

Table 2. **Mean values (x̄), standard deviation (SD) and number of metaphases (N) measured of chromosomes of *Eligmodontia* sp., expressed as a percentage of the female haploid set. Arm ratio = long arm/short arm**

Chromosome	N	Total Length x̄	Total Length SD	Arm Ratio x̄	Arm Ratio SD
1	10	10.9	.71	∞	
2	10	10.9	.33	∞	
3	10	10.0	.18	∞	
4	10	9.4	.29	∞	
5	10	9.0	.17	∞	
6	10	8.0	.47	∞	
7	10	5.2	.22	1.1	.07
8	10	5.0	.21	∞	
9	10	4.5	.28	∞	
10	10	4.2	.36	∞	
11	10	4.0	.22	∞	
12	10	3.6	.16	∞	
13	10	3.3	.26	∞	
14	10	3.3	.43	∞	
15	10	3.2	.24	∞	
X	10	5.8	.45	∞	
Y	10	3.4	.34	1.4	.20

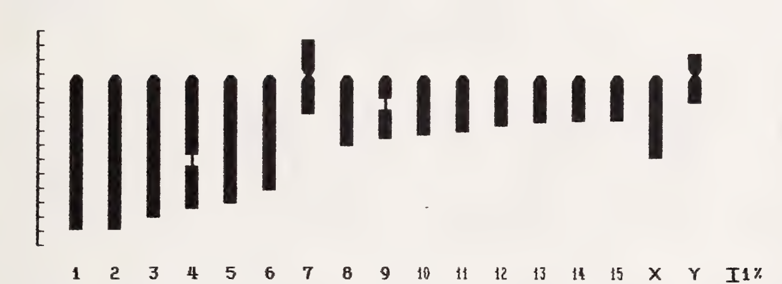


Fig. 8. Idiogram of *Eligmodontia sp.* 2n = 32, FNa = 32



Fig. 9. Bone marrow standard Giemsa staining karyotype of *Eligmodontia sp.* from Los Lagos, Neuquen Province, Argentina. 2n = 32; FNa = 32

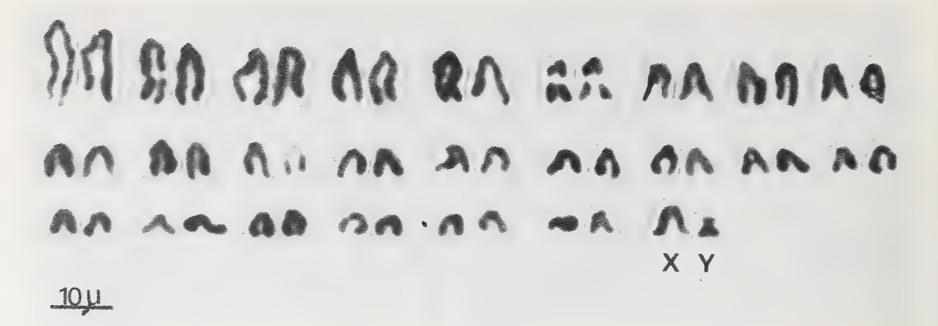


Fig. 10. Standard Giemsa staining karyotype of *Eligmodontia puerulus* from Ancomarca, Department of Puno, southern Peru. 2n = 50; FNa = 48

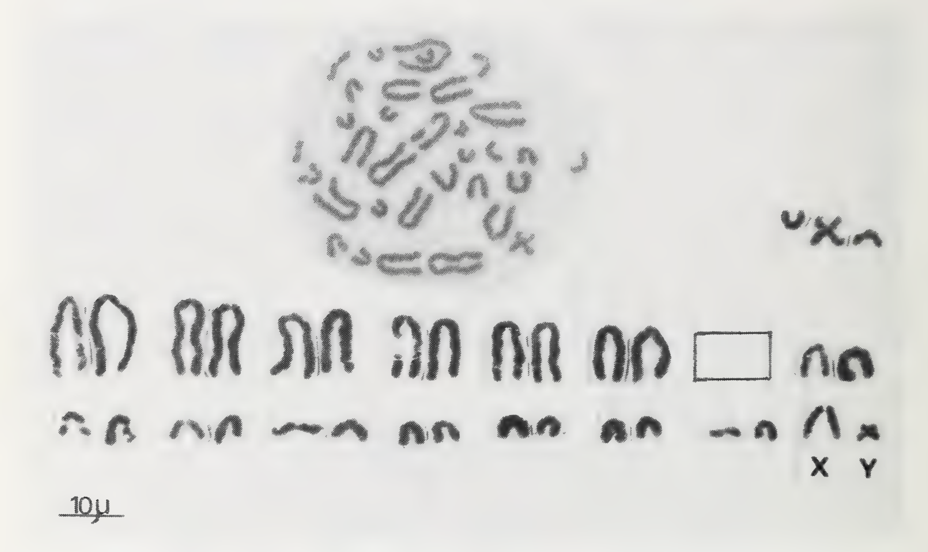


Fig. 11. Bone marrow standard Giemsa staining metaphase and karyotype of the polymorphic form of *Eligmodontia sp.* from Los Lagos, Neuquen Province, Argentina. 2n = 33; FNa = 32. Other indications as in Figure 6

The 2n = 33 karyotype shown by the remaining two individuals from Los Lagos has an extra pairs of telocentric and a single metacentric autosome. The sex chromosomes are as in the 2n = 32 karyotype. The metacentric odd element matches in size chromosomes of pair 7 of the "normal" karyotype. Chromosomes of the extra pair measure 2.57 %, roughly matching, therefore the size of the arms of the single metacentric (Fig. 11; Table 2). We can here also infer that the differences between the two karyotypes are due to one Robertsonian rearrangement.

Discussion

Karyotypic differences and their evolutionary consequences

We have thus demonstrated that the supposedly monotypic genus *Eligmodontia* shows a remarkable karyotypic polytypy, with populations showing 2n = 32–33, 2n = 43–44 and 2n

= 50 chromosomes. This situation is not peculiar, as phyllotine genera are known by their extreme interspecific chromosomal heterogeneity (MASSOIA et al. 1968; PEARSON 1972; WAINBERG and FRONZA 1974; PEARSON and PATTON 1976; GARDENAL et al. 1977; SPOTORNO and WALKER 1979; WALKER et al. 1979, 1984; WILLIAMS and MARES 1978; FORCONE et al. 1980; VITULLO et al. 1984; PEREZ ZAPATA et al. 1986).

Intrageneric karyotype heterogeneity in the Phyllotini is likely to be interpreted as following two different evolutionary patterns: mainly Robertsonian rearrangements and multiple type rearrangements. The first type is characteristic of *Phyllotis, Graomys* and *Auliscomys*, in which interspecific Robertsonian mutations leading to reproductive isolation *(Phyllotis)*, or extensive Robertsonian polymorphisms (*Graomys*, see WAINBERG and FRONZA 1974) are the rule. Interspecific Robertsonian rearrangements are also an acting force in some species of *Calomys*, but they are in most cases superimposed on more complex chromosomal repatternings (VITULLO and MERANI, pers. comm.). In this case, chromosomal homologies are almost impossible to detect, as between *Calomys laucha* (2n = 64) and *Calomys musculinus* (2n = 38). As is well known, chromosomal rearrangements of the fusion/fission Robertsonian type may not lead to reproductive isolation in all cases, the origination through this mechanism of a sterility barrier depending on the number and type of chromosomes involved (SPIRITO et al. 1981; GROPP and WINKING 1981; GROPP et al. 1982) or of the establishment of meiotic compensation mechanisms (WHITE 1978). When pericentric inversions and other chromosomal mutations are superimposed, however, the isolating effect of karyotypic differentiation is much more effective (REIG et al. 1980).

Although small Robertsonian rearrangements have been found in two of the known karyotypes of *Eligmodontia,* it is evident that the overall chromosomal differences between the three different karyotypes of this genus could hardly be thought of as resulting alone from fusion/fission processes. Even when we are lacking relevant banding information from two of them, the karyotypic comparisons oblige us to assume a complex array of chromosomal rearrangements, involving a combination of pericentric inversions, tandem translocations, and presumably, euchromatic amplifications and deletions. The scarcity of C-banding, and the almost exclusive pericentromeric nature of the heterochromatin, precludes ascribing an effective role to heterochromatin. It is legitimate to infer, therefore, that the pattern of chromosomal differentiation involved is the outcome of a long and complex history of chromosomal evolution, resulting in karyotypes which are now fully incompatible with interfecundity. Thus, we have to conclude that each of these karyotypes belongs to a different species of *Eligmodontia*.

Systematics and nomenclature

The problem is the name to apply to each of these species. We can tentatively propose species names from available ones from regions close to the localities of the different karyotypes. TATE (1932) and HERSHKOVITZ (1962) afforded a detailed taxonomic history of the available names for species of *Eligmodontia*.

The karyotype of 2n = 50 was referred by PEARSON and PATTON (1976) to *Eligmodontia typus*. As PEARSON (1951) had earlier referred specimens from southern Peru to *E. puerulus hirtipes*, this action meant the tacit acceptance of HERSHKOVITZ's (1962) lumping of *puerulus* Philippi as a subspecies of *typus*. However, both REISE (1973) and CORBET and HILL (1980) reestablished full species status for *puerulus* as OSGOOD (1943) and MANN (1945) did before. If we are to refer the 2n = 44 karyomorph to *E. typus*, as discussed below, there is no doubt that the 2n = 50 karyomorph of Peru has to be assigned to a species fully different from *typus*. The name *puerulus*, originally described from a specimen captured in San Pedro de Atacama, Antofagasta, Chile, at 3223 m a.s.l., would be indeed a reasonable option. As proposed by MANN (1945) and PEARSON (1951), other available

name from South of Peru, *E. hirtipes* Thomas 1902, is probably a mere subspecies of *puerulus*.

Of a more complex solution is the problem of the name to apply to the 2n = 44 karyomorph found in Chasicó and localities of Chubut Province. Since Chasicó is only 60 kms from Bahia Blanca, and Bahia Blanca is the type locality of *elegans*, this might be an available name for this form. However, *elegans* has been repeatedly considered as a synonym of *typus*, which has priority (Waterhouse 1839; Lesson 1842; Allen 1905; Hershkovitz 1962) and which was originally reported from "Buenos Aires". The further correction of the provenance of *typus* by D'Orbigny and Gervais (1847) as "province de Corrientes" was probably an error (Contreras pers. comm). Therefore it is reasonable to apply the name *typus* to the 2n = 44 karyomorph on the basis that one locality where it was found is close to the topotypical locality of *elegans*, which is a putative junior synonym of *typus*. The study of chromosomes of specimens from other areas in Buenos Aires Province may be critical to corroborate this decision.

As regards the 2n = 32–33 karyomorph from Los Lagos, Neuquen, its species assignment is a matter of serious doubt. The only available name in Patagonia for a species of *Eligmodontia* is *E. morgani* Allen 1901, from Arroyo Else, in north-western Santa Cruz. There is the antecedent that Biraben and Scott (1936) referred to *morgani* specimens found in Pilcaniyeu, Rio Negro, not very far from Los Lagos, Neuquen. However, specimens reported here from Pampa de Salamanca, which is closer to Arroyo Else than Los Lagos, showed the 2n = 44 karyotype we assigned to *E. typus*, and the same happens with specimens from the intermediate locality of Paso del Indio. Additionally, it seems that a single species of *Eligmodontia* inhabits the south and the east central Patagonia, and therefore, *morgani* may be a junior synonym of *typus*. Assuming this, we prefer not to assign any specific name to the species living in Los Lagos, Neuquen, showing the peculiar 2n = 32–33 karyotype which exludes its classification either as *E. puerules* or *E. typus*.

Acknowledgements

We specially thank Dr. Oliver P. Pearson for providing negatives of the karyotype of the Peruvian *Eligmodontia*, and for suggestions. We also thank Juan J. Bianchini for help in identifying the Chasicoan specimens. We acknowledge John A. W. Kirsch, Orlando A. Scaglia, Carlos Velazquez, Sylvia Dahinten, Roberto Taylor, Diana Aloia, Susana Pedrazza, Alicia Toyo, Atila Gosztony, G. Pognoni, and J. Garrido for help during field work and for capture of specimens. Maria Alicia Barros, Luisa Kuba and Maria Beatriz Espinosa helped in laboratory work. This paper was partially financed by CONICET grant PID Nr. 3-085-300/85 given to O. A. Reig, CONICET grant PID Nr. 3-079700/85 given to R. L. Wainberg, and C.I.C. grant Nr. 21090102/85 given to R. L. Wainberg and M. L. G. de Fronza.

Resumen

Multimorfismo cromosómico y polimorfismo autosómico en Eligmodontia (Cricetidae, Sigmodontinae)

Se estudiaron los cariotipos de médula osea y de gonadas masculinas, y las bandas G- y C- en roedores filotinos del genero *Eligmodontia* de diferentes localidades de Argentina. Veintiocho ejemplares de Chasicó, en el sur de la Provincia de Buenos Aires y del noreste, sudeste y centro de la provincia de Chubut mostraron un cariotipo de 2n = 44, Fn = 44, constituido por un par de grandes metacéntricos y veinte pares de telocéntricos mucho mas pequeños, y un sistema sexual X-Y. Un individuo de Chasicó mostró una variante robertsoniana del mismo cariotipo, de 2n = 43 cromosomas. Tres ejemplares de Los Lagos, Provincia de Neuquen, demostrarom poseer un cariotipo polimorfico completamente diferente del anterior, de 2n = 32–33, consistente al estado homocigótico de 14 pares de autosomas telocéntricos, un par de metacéntricos pequeños y el par sexual. Se ilustra, además, el cariotipo de 2n = 50, FNa = 48 de Perú, dado a conocer someramente por Pearson y Patton, y se lo compara con los dos anteriores. Se sostiene la hipótesis de que estos tres diferentes citotipos corresponden a tres diferentes especies. De manera que *Eligmodontia*, clasicamente considerado un género momotípico, resultaría politípico. Se proponen provisionalmente los nombres de *Eligmodontia typus* para el citotipo de las provincias de Buenos Aires y Chubut, y de *Eligmodontia puerulus* para el

de Peru. Se discute el nombre que debería-corresponder al citotipo de Neuquen, considerandose que el problema no puede resolverse por ahora.

Zusammenfassung

Chromosomale Vielfalt und autosomaler Polymorphismus bei Eligmodontia (Cricetidae, Sigmodontinae)

Chromosomenbilder aus Knochenmark und Hoden von Nagern der Gattung *Eligmodontia* aus verschiedenen Gebieten Argentiniens wurden untersucht, zum Teil in Präparaten nach G- und C-Bandenfärbung. 28 Exemplare aus den Provinzen Buenos Aires und Chubut besaßen 2n = 44 Chromosomen (FNa = 44). Ein sehr großes Autosomenpaar war metazentrisch, die übrigen 20 Autosomenpaare waren sehr viel kleiner und telozentrisch. Ein Tier von Chasico hatte offenbar als Folge einer Robertsonschen Fusion nur 43 Chromosomen. Drei Exemplare aus Los Lagos, Provinz Neuquen, zeigten einen ganz anderen Karyotyp: 2n = 32–33; bei 32 Chromosomen waren 14 Autosomenpaare telozentrisch, ein kleines Paar metazentrisch. Bei dem Tier mit 33 Chromosomen entsprachen einem metazentrischen Autosom zwei kleine, bei den anderen Exemplaren nicht vorhandene telozentrische. Aus Peru ist ein weiterer Karyotyp (2n = 50; FNa = 48) von Pearson und Patton (1976) beschrieben worden. Wir nehmen an, daß die drei Chromosomen-Typen drei verschiedenen Arten angehören, daß also *Eligmodontia* nicht nur eine Art enthält, wie bisher angenommen wurde, sondern mindestens drei. Wir beziehen den Namen *Eligmodontia typus* auf die Populationen mit 44 Chromosomen, *E. puerulus* auf den Typ mit 50 Chromosomen. Der Namen der Form mit 32 Chromosomen bleibt noch zu klären.

Literature

Allen, J. A. (1905): Mammalia of southern Patagonia. Reports of the Princeton University Expeditions to Patagonia, 1896–1899, **3**, 263–310.

Biraben, M.; Hilton Scott, M. (1937): Viaje alrededor de Santa Cruz. Revista del Museo de la Plata (N. Serie), Seccion Oficial 1936, 93–164.

Corbet, G. B.; Hill, J. E. (1980): A world list of mammalian species. London: British Museum (Nat. Hist.) and Ithaca, N. Y.: Cornell Univ. Press.

D'orbigny, A. D.; Gervais, P. (1847): Voyage a l'Amerique Meridionelle. IV. Mammifères. Paris.

Evans, E. P.; Breckon, G.; Ford, C. E. (1964): An air-drying method for meiotic preparation from mammalian testes. Cytogenetics **3**, 289–294.

Forcone, A. E.; Luna, M. V.; Kravetz, F. O.; Lisanti, J. A. (1980): Bandas C y G de *Calomys musculinus* (Rodentia, Cricetidae). Mendeliana **4**, 57–65.

Gardenal, C. N.; T. de Juarez, N.; Gutierrez, M. (1977): Contribución al conocimiento de tres especies del género *Calomys* (Rodentia, Cricetidae). 1. Estudios citogeneticos. Physis **36**, 169–178.

Gropp, A.; Winking, H. (1981): Segregational patterns and biological consequences of Robertsonian translocations, Cytology, meiosis. In: Biology of the house mouse. Ed. by J. R. Berry. New York: Academic Press. 141–181.

Gropp, A.; Winking, H.; Redi, C. (1982): Consequences of Robertsonian heterozygosity: segregational impairment of fertility versus male-limited sterility. In: Genetic control of gamete production and function. Ed. by Crossignani and S. Rubin. New York: Academic Press. 114–134.

Hershkovitz, P. (1962): Evolution of neotropical cricetine rodents (Muridae), with special reference to the phyllotine group. Fieldiana, Zoology **46**, 1–524.

Hurtado de Catalfo, G.; Wainberg, R. L. (1977): Cytogenetics of rodents of the genus *Eligmodontia* (Cricetidae). In: Joint Seminar and Workshop: Aspects of Chromosome Organization and Function, III Latin American Congress of Genetics. Ed. by M. E. Drets, N. Brum Zorrilla, and G. A. Folle. Montevideo. 237.

Levan, A.; Fredga, K.; Sandberg, A. A. (1964): Nomenclature for centromeric position on chromosomes. Hereditas **52**, 201–220.

Lesson, R. M. (1842): Nouveau tableau du regne animal. Mammifères. Paris: Arthus Bertrand.

Mann, F. G. (1945): Mamíferos de Tarapacá. Biologica, Santiago, **2**, 23–134.

Mares, A. N. (1975): Observations of Argentine desert rodent ecology, with emphasis on water relations of *Eligmodontia typus*. In: Rodents in desert environments. Ed. by I. Prakash and P. K. Ghosh. 155–175.

— (1977): Water economy and salt balance in a South American desert rodent, *Eligmodontia typus*. Bioch. Physiol. **56A**, 325–332.

Massoia, E.; Fornes, A.; Wainberg, R. L.; Gentile de Fronza, T. (1968): Nuevos aportes al conocimento de las especies del género *Calomys* (Rodentia, Cricetidae). Rev. Inv est. Agrop. **5**, 63–92.

Osgood, W. H. (1943): The mammals of Chile. Field Museum Nat. Hist., Zool. ser. **30,** 1–268.
Pearson, O. P. (1951): Mammals in the highlands of southern Peru. Bull. Mus. Comp. Zool. **106,** 117–134.
— (1972): New information on ranges and relationships within the rodent genus *Phyllotis* in Peru and Ecuador. J. Mammalogy **53,** 677–686.
Pearson, O. P.; Patton, J. L. (1976): Relationships among South American phyllotine rodents based on chromosome analysis. J. Mammalogy, **57,** 339–350.
Perez-Zapata, A.; Vitullo, A.; Reig, O. A. (1987): Karyotypic and sperm distinction of *Calomys hummelincki* from *Calomys laucha* (Rodentia: Cricetidae). Acta Cient. Venezol. **38,** 90–93.
Reig, O. A. (1981): Modelos de especiacion cromosómica en las casiraguas (género *Proechimys*) de Venezuela. In: Ecology and genetics of animal speciation. Ed. by O. A. Reig. Caracas: Equinoccio. 149–190.
— (1984): Significado de los métodos citogéneticos para la distinción y la interpretación de las especies, con especial referencia a los mamíferos. Rev. Mus. Argentino C. Nat. "B. Rivadavia" e Inst. Nac. Inv. Cienc. Nat., Zool. **13,** 19–44.
— (1986): Diversity Patterns and Differentiation of High Andean Rodents. In: High Altitude Tropical Biogeography. Ed. by F. Vuilleumier and M. Monasterio. New York, Oxford: Oxford Univ. Press. 404–439.
Reig, O. A.; Aguilera, M.; Barros, M. A.; Useche, M. (1980): Chromosomal speciation in a Rassenkreis of Venezuelan spiny rats (genus *Proechimys*, Rodentia, Echimyidae). Genetica **52/53,** 291–312.
Reig, O. A.; Olivo, N.; Kiblishky, P. (1971): The idiogram of the Venezuelan vole mouse, *Akodon urichi venezuelensis* Allen (Rodentia, Cricetidae). Cytogenetics **10,** 99–114.
Reise, D. (1973): Clave para la determinación de los craneos de marsupiales y roedores chilenos. Gayana, Instituto de Concepción **17,** 1–20.
Rothfels, K. H.; Siminovitch, L. (1958): An air-drying technique for flattening chromosomes in mammalian cells grown *"in vitro"*. Stain Technol. **33,** 73–77.
Seabright, M. (1971): A rapid banding technique for human chromosomes. Lancet **2,** 971–972.
Spirito, F.; Modesti, A.; Perticone, P.; Cristaldi, M.; Federici, F.; Rizzoni, M. (1980): Mechanisms of fixation and accumulation of centric fusions in natural populations of *Mus musculus* L. I. Karyological analysis of hybrid zone between two populations in the central Apennines. Evolution **43,** 453–466.
Spotorno, A. E.; Walker, L. (1979): Análisis de similitud cromosómica según patrones de bandas G en cuatro especies chilenas de *Phyllotis* (Rodentia, Cricetidae). Arch. Biol. Med. Exper. **12,** 83–90.
Sunmer, A. T. (1972): A simple technique for demonstrating centromeric heterochromatin. Exp. Cell. Res. **75,** 304–306.
Tate, G. H. H. (1932): The taxonomic history of the South American cricetid genera *Euneomys* (subgenera *Euneomys*) and *Galenomys, Auliscomys, Chelemyscus, Chinchillula, Phyllotis, Paralomys, Graomys, Eligmodontia* and *Hesperomys*. Amer. Mus. Novitates **541,** 1–21.
Vitullo, A.; Kajon, A. E.; Percich, R.; Zuleta, G.; Merani, M. S.; Kravetz, F. (1984): Caracterización citogenética de tres especies de roedores (Rodentia, Cricetidae) de la República Argentina. Rev. Mus. Arg. Cien. Nat. "Bernardino Rivadavia" (Zool), **13(52),** 491–498.
Wainberg, R. L.; Gentile de Fronza, T. (1974): Autosomic polymorphism in *Phyllotis griseoflavus griseoflavus* Waterhose 1837 (Rodentia, Cricetidae). Boll. Zool. **41,** 19–24.
Walker, L. I.; Spotorno, A. E.; Fernandez-Donoso, R. (1979): Conservation of whole arms during chromosomal divergence of phyllotine rodents. Cytog. Cell Genet. **24,** 209–216.
Walker, L. I.; Spotorno, A. E.; Arrau, J. (1984): Cytogenetic and reproductive studies of two nominal subspecies of *Phyllotis darwini* and their experimental hybrids. J. Mammalogy **65,** 220–230.
Waterhouse, G. R. (1839): The zoology of the voyage of H.M.S. Beagle. Pt. 2. Mammalia. London: Smith, Elder and Co.
White, M. J. D. (1978): Modes of Speciation. San Francisco: Freeman.
Williams, D. F.; Mares, M. A. (1978): A new genus and species of phyllotine rodent (Mammalia: Muridae) from northwestern Argentina. Ann. Carnegie Mus. **47,** 193–221.

Authors' addresses: Marcelo O. Ortells, and Osvaldo A. Reig, GIBE, Departamento de Ciencias Biológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Pabellón 2, Ciudad Universitaria Nuñez, RA-1428 Buenos Aires, Argentina; Ricardo L. Wainberg, Graciela E. Hurtado de Catalfo, and Teresa M. L. Gentile de Fronza, Cátedra de Biología General, Departamento de Ciencias Biológicas, Facultad de Ciencias Exactas, Universidad Nacional de La Plata, RA-1900 La Plata, Provincia de Buenos Aires, Argentina

Z. Säugetierkunde 54 (1989) 141–152

ISSN 0044-3468

Chromosomal banding comparisons among American and European Red-backed mice, genus *Clethrionomys*

By W. S. Modi and Roswitha Gamperl

Biological Carcinogenesis Development Program, Program Resources, Inc., Frederick Cancer Research Facility, Frederick, USA and Institut für Medizinische Biologie und Humangenetik der Universität Graz, Austria

Receipt of Ms. 29. 10. 1987

Abstract

G-banded chromosomes are presented for five species of *Clethrionomys: C. glareolus, C. rufocanus, C. gapperi, C. californicus,* and *C. rutilus.* Similar data are available in the literature regarding *C. andersoni.* The presence of a shared derived autosomal reciprocal translocation allies *C. glareolus, C. gapperi, C. californicus* and *C. rutilus,* while the primitive condition is retained in *C. rufocanus* and *C. andersoni.* Intraspecific and interspecific variability in C-banding patterns is limited. Variation in Y chromosome size and/or morphology apparently occurs convergently in populations of three species. Interspecific chromosomal variation is much less in *Clethrionomys* than in other genera of arvicolid rodents, and *Clethrionomys* have speciated without concomitant structural chromosomal differences. Ribosomal DNA (rDNA) transcriptional activity was assayed among five different tissues from individuals belonging to three species using the silver staining procedure. Fibroblast cells had a significantly greater number of nucleolus organizer regions (Ag–NORs) than did femur bone marrow cells from the same specimen. Among similar tissues, intraspecific variability in the mean number of NORs per cell may be equal to or greater than interspecific differences. Sister chromatid exchange was measured in a lung fibroblast cell line of *C. rutilus* using 5-bromodeoxyuridine (BrdU) incorporation. The mean number of exchanges per cell (8.0) was found to be equal to or less than that reported in studies of other rodents. Meiotic chromosome analyses of *C. californicus* indicate that a sex vesicle is present during pachytene and that end-to-end association between the centromeric region of the acrocentric X and the small-sized, C-band negative Y occurs in diakinesis.

Introduction

The Holarctic rodent genus *Clethrionomys* (family Arvicolidae) is currently thought to contain seven (Honacki et al. 1982) or eight (Corbet 1978) species. These species are difficult to distinguish morphologically, and controversy has traditionally existed among classical taxonomists regarding the systematics of the group. Several of these species have fairly broad geographic distributions in either Eurasia (*C. glareolus* and *C. rufocanus*) or North America *(C. gapperi),* while one species *(C. rutilus)* exhibits a circumpolar distribution. The remaining forms are much more restricted in distribution either in the Palearctic *(C. andersoni, C. centralis, C. sikotanesis)* or in the Nearctic *(C. californicus).* Habitats occupied by these animals are principally mesic situations in coniferous, deciduous and mixed forests where an abundant litter is available, although the more specialized *C. rutilus* is found in a boreal, tundra habitat.

Previous comparative analyses have indicated that species in the family Arvicolidae exhibit some of the most extreme interspecific karyotypic variability yet observed among vertebrates (summarized by Modi 1987a). In this vein, the present study was undertaken because several earlier studies have suggested that species of *Clethrionomys* may be much more chromosomally conservative than are some closely related genera (Gamperl 1982a; Obara 1986). Results from the comparative analyses of G-banding and C-banding patterns from a total of six species (including information derived from the literature) are presented and compared with systematic arrangements of the genus that are based upon

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5403-0141 $ 02.50/0

other types of data. Additionally, results from silver-staining for the nucleolus organizer region, sister chromatid exchange and investigations on meiotic chromosomes are presented for several of these species.

Materials and methods

Karyotypic analyses were carried out on 17 specimens belonging to five species. Cells for chromosome preparations from *C. glareolus* and *C. rufocanus* were obtained from fibroblast cultures initiated from ear biopsies, grown in TC Medium Eagle, Earle BSS and supplemented with 20 % fetal calf serum. Cells from *C. rutilus* and all specimens of *C. gapperi* were obtained from fibroblast cultures initiated either from lung or ear biopsies and grown in McCoy's 5 A modified medium supplemented with 10 % fetal calf serum. Metaphase cells from three of the five specimens of *C. gapperi* were also derived from femur bone marrow following the yeast pretreatment procedure (Lee and Elder 1980), while preparations from *C. californicus* were obtained from spleen tissue (Modi 1985), femur bone marrow, or vertebral column bone marrow. Metaphase cell harvest, incubation, fixation, and slide preparation followed standard procedures. Slides were aged at 37 °C for 2–20 days before being banded.

G-bands were obtained on preparations from *C. glareolus* and *C. rufocanus* using a slightly modified version of the ASG technique (Sumner et al. 1971). Slides were incubated in 2× SSC (pH 7.0) at 60 °C for 8–16 h before being stained in 2 % Giemsa in sodium phosphate buffer (pH 6.8). G-bands from *C. gapperi, C. californicus* and *C. rutilus* were obtained by digestion with 0.025 % tgrypsin in Hanks' balanced salt solution for 20–200 sec, followed by dehydration in ethanol prior to staining in Giemsa (Seabright 1971). In Fig. 1 G-banded chromosomes are numbered following the designations proposed as phylogenetically primitive for the family Arvicolidae as defined by Modi (1987a). The chromosomes of *C. rufocanus* are arranged according to length, and the homologous elements from the other species paired accordingly (Fig. 1c).

C-bands were obtained from specimens of all five species following a variant of the BSG procedure of Sumner (1972). Slides were treated in 0.2 N HCl for 1 hr, followed by treatment in saturated $Ba(OH)_2$ for 2–20 min at 37 °C or 50 °C. Slides were then covered with 2× SSC and incubated at 60 °C for 1 hr prior to dehydration in ethanol and staining in 4 % Giemsa. Ag-NORs were obtained on the chromosomes of *C. gapperi, C. californicus* and *C. rutilus* following the AG-1 procedure of Bloom and Goodpasture (1976). Slides were flooded with a 50 % solution of $AgNO_3$ containing 0.03 % formalin and incubated at 60 °C for 1–4 hr. At least 50 silver-stained cells were examined per specimen and the number of chromosomes staining positively in each cell was recorded.

The frequency of sister chromatin exchange in a lung fibroblast cell line from *C. rutilus* was analyzed following a slight modification of the procedure of Perry and Wolff (1974). Cells were grown in the dark for 30 hr with 5-bromodeoxyuridine (BrdU) at a concentration of 30 µg/ml. Following slide preparation chromosomes were stained with Hoechst 33 258 (1 µg/ml) for 15 min, rinsed, dried and then flooded with 2× SSC and illuminated with long-wave UV light for 1 hr. Slides were stained in 2 % Giemsa in phosphate buffer (pH 6.8) for 2–4 min.

Finally, meiotic chromosomes were obtained from one male *C. californicus*. Seminiferous tubules were minced with curved scissors in a watch-glass in 2 ml of 0.7 % sodium citrate. An additional 8 ml of sodium citrate solution was added, and the mixture incubated at 37 °C for 25 min. Subsequent fixation and slide preparation followed traditional procedures.

The following specimens were examined: *C. rufocanus,* Sweden: Gällivare, 1 male. *C. glareolus,* Austria: Graz, 1 male, 1 female. Salzburg, 1 male. France: Savoie, 1 male, 2 females. *C. gapperi,* USA: Vermont, Chittenden Co., 1 male, 1 female. West Virginia, Randolph Co., 1 male; Virginia, Highland Co., 2 females. *C. californicus,* USA: Oregon, Tillamook Co., 1 male. Linn Co., 1 male, 2 females. *C. rutilus,* USA: Alaska, Fairbanks, 1 male.

Results

G-banded karyotypes were analyzed for all five species, including populations of *C. gapperi* from Vermont and Virginia and specimens of *C. glareolus* from two localities in Austria and one in France. No intraspecific differences in G-banding patterns were observed in either of these two species. Representative G-banded preparations for *C. rutilus* and *C. gapperi* are presented in Figures 1a–b. Illustrated in Figure 1c is a composite karyotype comparing the haploid complement from each of the five species. All species have 2n = 56, NF_a = 56 with 25 pairs of acrocentric and one pair of small metacentric autosomes. Among the autosomes, pairs 1 and 9 of *C. rufocanus* differ from homologous

Eine Information der Verlagsbuchhandlung PAUL PAREY Berlin und Hamburg

Pareys Studientexte 65

Helmut Niepage

Methoden der praktischen Hämatologie für Tierärzte

2. Auflage

Helmut Niepage

Methoden der praktischen Hämatologie für Tierärzte



Ergänzende Fachliteratur:

Colour Atlas for the Diagnosis of Bacterial Pathogens in Animals
Farbatlas zur Diagnose bakterieller Infektionserreger der Tiere
Von Prof Dr W Bisping, Hannover, und Prof Dr Dr G Amtsberg, Hannover 1988 339 Seiten mit 223 Abbildungen, davon 180 farbig, und 96 Tabellen. Gebunden DM 358,- (zweisprachig Englisch/Deutsch). ISBN 3-489-50716-9

Handbuch der Schutzimpfungen in der Tiermedizin
Von Prof Dr Dr h.c. A Mayr, München, Prof. Dr G. Eißner, Tübingen, und Prof Dr. B. Mayr-Bibrack, München 1984 1026 Seiten mit 155 teilweise farbigen Abbildungen, davon 50 auf 8 Farbtafeln Gebunden DM 198,- ISBN 3-489-66416-7

Labordiagnostik für die tierärztliche Praxis
Von Prof Dr H Plonait, Hannover. 1980. 148 Seiten mit 29 Abbildungen und 25 Tabellen Gebunden DM 48,- ISBN 3-489-74916-2

Atlas zur Hämatologie von Hund und Katze
Atlas of Hematology of the Dog and Cat
Von Dr P Keller Basel, und Prof Dr U Freudiger, Bern 1983 160 Seiten mit 284 Abbildungen in 665 Einzeldarstellungen, davon 381 farbig, einer schematischen Zeichnung und 2 Tabellen Gebunden DM 218,- (fünfsprachig: Deutsch, Englisch, Französisch, Italienisch, Spanisch) ISBN 3-489-65516-8

Praktikum der Hundeklinik
Von Dr H G Niemand, Mannheim. 6., völlig neubearbeitete Auflage herausgegeben von Prof Dr P F Suter, Zürich. 1989. 848 Seiten mit 375 Abbildungen, davon 49 farbig, und 97 Tabellen Gebunden DM 198,- ISBN 3-489-50816-5

Kompendium der allgemeinen Virologie
Pareys Studientexte, Nr. 4
Von Prof Dr M C. Horzinek, Utrecht Unter Mitarbeit von Dr B A M van der Zeijst, Utrecht, und Prof Dr J van der Want, Wageningen 2., neubearbeitete Auflage. 1985 159 Seiten mit 86 Abbildungen und 16 Tabellen. Kartoniert DM 29,- ISBN 3-489-68116-9

Kompendium der allgemeinen medizinischen Bakteriologie
Pareys Studientexte Nr. 19
Von Prof Dr H Fey, Bern 1978 227 Seiten mit 77 Abbildungen und 13 Tabellen Kartoniert DM 28,- ISBN 3-489-61516-6

Kompendium der allgemeinen Immunologie
Pareys Studientexte, Nr. 20
Von Dr R von Fellenberg, Zürich 1978 201 Seiten mit 64 Abbildungen, 21 Tabellen, und 2 Anhängen (28 Tabellen). Kartoniert DM 29,- ISBN 3-489-61416-X

Kompendium der medizinischen Mykologie
Pareys Studientexte, Nr. 25
Von Prof Dr B. Gedek, München. 1980 395 Seiten mit 195 Abbildungen, davon 8 farbig und 34 Tabellen Kartoniert DM 48,- ISBN 3-489-62816-0

Kompendium der veterinärmedizinischen Bakteriologie
Pareys Studientexte, Nr. 45
Von Prof Dr J Nicolet Bern 1985 280 Seiten mit 26 Abbildungen und 71 Tabellen Kartoniert DM 38,- ISBN 3-489-69416-3

Bestellschein

1186/IV/89

Hiermit bestelle ich aus dem Verlag Paul Parey Berlin und Hamburg Spitalerstr 12 2000 Hamburg 1 zur Lieferung durch:

___ **Expl. Niepage, Methoden der praktischen Hämatologie für Tierärzte DM 34,-**
___ Expl.
___ Expl. Sammelverzeichnis Veterinärmedizin, Auswahl 1989 kostenlos

Name/Anschrift ____________________

Datum/Unterschrift ____________________

Pareys Studientexte, Nr. 65

Von Prof. Dr. Helmut Niepage, Berlin. 2., neubearbeitete Auflage. 1989. 78 Seiten mit 18 Abbildungen. 23,5 x 15,5 cm. Kartoniert DM 34,— ISBN 3-489-51416-5

Methoden der praktischen Hämatologie - das sind nicht nur die labortechnischen Verfahren, sondern neben der sorgfältigen Gewinnung auch die kritische Beurteilung hämatologischer Daten in der tierärztlichen Praxis und im Tierversuch, um anhand von Blutproben den Funktionszustand lebenswichtiger Zellsysteme zu erkennen und diagnostisch auszuwerten.

Da die Hämatologie während des tierärztlichen Studiums oft zu kurz kommt, bietet das Buch, bereits in der zweiten, neubearbeiteten Auflage, eine anwendungsbezogene Einführung in die spezielle Hämatologie für Tierärzte und Studierende. Es ist zugleich ein praktischer Ratgeber fürs Labor.

Aus dem Inhalt:

Handwerk: Hämatokrit ("Blutscheidung") - Zählung der Blutkörperchen - Zählung der Blutplättchen - Hämoglobinbestimmung - Indices für Größe, Hämoglobingehalt und Farbe der Erythrocyten - Blutausstrich und Differentialblutbild - Zählung der Retikulocyten - Osmotische Resistenz (Fragility) - Erythrocytendurchmesser - Dicker Tropfen - Senkungsgeschwindigkeit der Blutkörperchen - Knochenmark - Lymphknoten. Meßfehler. Cytomorphologie: Retikulum des Knochenmarks - Hämopoetische Stammzellen - Erythrozyten - Neutrophile - Eosinophile - Lymphocyten - Thrombocyten. Status: Blutstatus (Hämogramm) - Knochenmarkstatus (Myelogramm) - Lymphknotenstatus. Norm. Schlußsätze. Literaturverzeichnis. Stichwortverzeichnis.

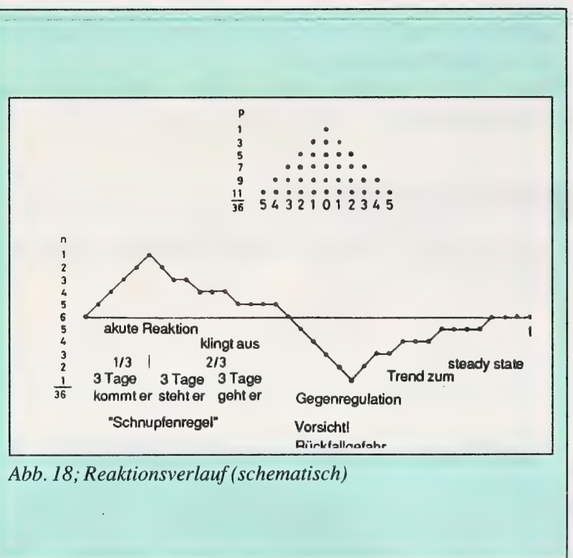


Abb. 18; Reaktionsverlauf (schematisch)

elements in the karyotypes of the other four species by a reciprocal translocation. Complete homology appears to exist among the remaining autosomes and the X chromosome in all species, however, the variable quality of banding of several smaller-sized pairs from *C. rufocanus* (nos. 17, 22, and 25) makes these comparisons equivocal. Intraspecific and interspecific variability exists in the size and morphology of the Y chromosome. The Y in *C. rufocanus* and *C. gapperi* is a medium sized acrocentric. In *C. glareolus* from Austria and in *C. rutilus* it is metacentric, while in the *C. glareolus* specimen from France the element is submetacentric. The Y in *C. californicus* is an extremely small-sized acrocentric.

C-bands were examined from all five species, including specimens of *C. glareolus* from Austria and France, and *C. gapperi* from Vermont, Virginia and West Virginia. Presented in Figures 2a–b are C-banded karyotypes of *C. gapperi* and of *C. rutilus*, while C-banded karyotypes of *C. rufocanus, C. glareolus* and *C. californicus* are found elsewhere (Gamperl 1982a; Modi 1987b). Among all species, autosomal C-bands are found predominantly centromerically. The sizes of centromeric autosomal C-bands in *C. rufocanus* and *C. glareolus* (Austria) are larger than those in the other species or in the French specimen of *C. glareolus*. Further, both members of pair 27 in *C. rufocanus* are almost completely C-band positive. In the specimen of *C. gapperi* from West Virginia two different pairs of autosomes exhibit C-band heteromorphisms. In the first pair, one element has a large-sized centromeric C-band and C-band positive short arms, both of which are absent in the homologue. In the second pair, one element is completely heterochromatic (Fig. 2a). The other specimens of *C. gapperi* did not show this intraindividual C-band variation. The Y is completely C-band positive in all species except *C. californicus*, where it is C-band negative.

Metaphase cells from a total of five different tissues (femur bone marrow, vertebral column bone marrow, spleen, ear fibroblasts, and lung fibroblasts) from six specimens belonging to three species (*C. gapperi, C. californicus,* and *C. rutilus*) were examined using silver staining (s. Table). Representative cells from *C. gapperi* and *C. californicus* are shown in Figs. 2c–d. All Ag-NORs examined were found pericentromerically and never interstitially or telomerically. The mean number of Ag-NORs per cell ranged from 2.46 to 3.25 for femur bone marrow cells among the four specimens examined, and from 5.58 to 8.37 for fibroblast cells among the three specimens examined. The modal number of Ag-NORs per cell was lower for femur bone marrow cells than for cells from the other tissue types. The range between the minimum and maximum number of NORs staining per cell showed little variability among all specimens and tissues examined (s. Table).

Differences among the mean number of NORs staining per cell (s. Table) were tested for statistical significance using a one-way analysis of variance (ANOVA) in each of the following five comparisons: 1. *C. gapperi* 6 femur bone marrow versus ear fibroblast cells ($F = 106.9$, $p < 0.001$), 2. *C. gapperi* 7 femur bone marrow versus ear fibroblast cells ($F = 257.5$, $p < 0.001$), 3. *C. californicus* 3 femur bone marrow versus spleen cells ($F = 0.53$, $p > 0.10$), 4. femur bone marrow cells from *C. gapperi* 6, *C. gapperi* 7, *C. californicus* 2 and *C. californicus* 3 ($F = 3.34$, $0.02 < p < 0.05$) and 5. fibroblast cell lines from *C. gapperi* 6, *C. gapperi* 7 and *C. rutilus* 1 ($F = 78.79$, $p < 0.001$). These results indicate significant differences among group means in all analyses except the comparison of *C. californicus* 3 femur bone marrow versus spleen cells.

Next, two of the above analyses were repeated after deleting one sample from each. Three of the four femur samples (all except *C. californicus* 2) were compared and a lack of significance was found ($p > 0.10$). Similarly, two of the three fibroblast samples (except *C. gapperi* 6) were compared and the ANOVA was non-significant ($p > 0.10$). These last two analyses indicate that the two deleted samples differ significantly from the remaining samples in their respective groups which collectively represent rather homogeneous populations. The frequency distributions of the samples analyzed by the ANOVAs are plotted in Fig. 4.



Fig. 1. G-banded karyotypes of *Clethrionomys.* a: Male *C. rutilus;* b: Haploid complements of a female *C. gapperi* from Vermont at three different stages of condensation; c: Composite karyotype comparing the haploid complement from each of five species. Elements, arranged from left to right in each set, are from *C. rufocanus, C. glareolus, C. gapperi, C. californicus,* and *C. rutilus.* Asterisks indicate chromosomes that have undergone rearrangement from the primitive condition as proposed by Modi (1987a)

Table. **Results from the silver staining analyses for the nucleolus oganizer region**
Standard statistics regarding the number of Ag-NORS per cell among different tissues are given for three species of *Clethrionomys*

Specimen	Tissue	No. Cells	Mean	SD	Mode	Range
C. gapperi 6	f[1]	241	2.80	2.58	0	0–12
C. gapperi 6	e	169	5.58	2.78	6	0–11
C. gapperi 7	f	298	3.24	2.88	0	0–12
C. gapperi 7	e	117	8.37	3.05	10	0–13
C. californicus 2	f	141	2.46	2.07	2	0–9
C. californicus 3	f	115	3.25	3.07	0	0–11
C. californicus 3	s	105	3.54	2.80	3	0–12
C. californicus 4	v	123	5.16	3.22	3	0–13
C. rutilus 1	l	51	8.28	2.52	10	0–13

[1] Tissue sources from which metaphase chromosomes were derived: f = femur bone marrow, e = ear fibroblast cell line, s = spleen, v = vertebral column bone marrow, l = lung fibroblast cell line



Fig. 2. a: C-banded karyotype of a male *C. gapperi* from West Virginia with the arrowheads illustrating autosomal C-band heteromorphisms; b: C-banded karyotype of a male *C. rutilus*; c: Silver stained metaphase cell of female *C. gapperi* 7 from Vermont derived from an ear fibroblast cell line; d: Silver stained metaphase cell from female *C. californicus* 4 derived from vertebral bone marrow. In both (c–d) Ag-NORs are visible at the centromeres of eleven acrocentric chromosomes

The frequency of sister chromatid exchange was recorded from 16 cells in a male specimen of *C. rutilus*. A representative metaphase cell is shown in Figure 3a. The mean number of exchanges per cell plus or minus one standard deviation was 8.0 ± 3.3 with a range of 5–14.

A total of 21 pachytene and 11 diakinesis cells was observed in meiotic preparations from a single male *C. californicus*. Twenty-seven autosomal bivalents and a conspicuous sex vesicle were observed in the pachytene cells (Fig. 3b). At diakinesis 27 autosomal bivalents were apparent, and an end-to-end association existed between the X and Y (Fig. 3c). It appears as though the centromeric end of the X synapses with the Y in the Giemsa stained cells.

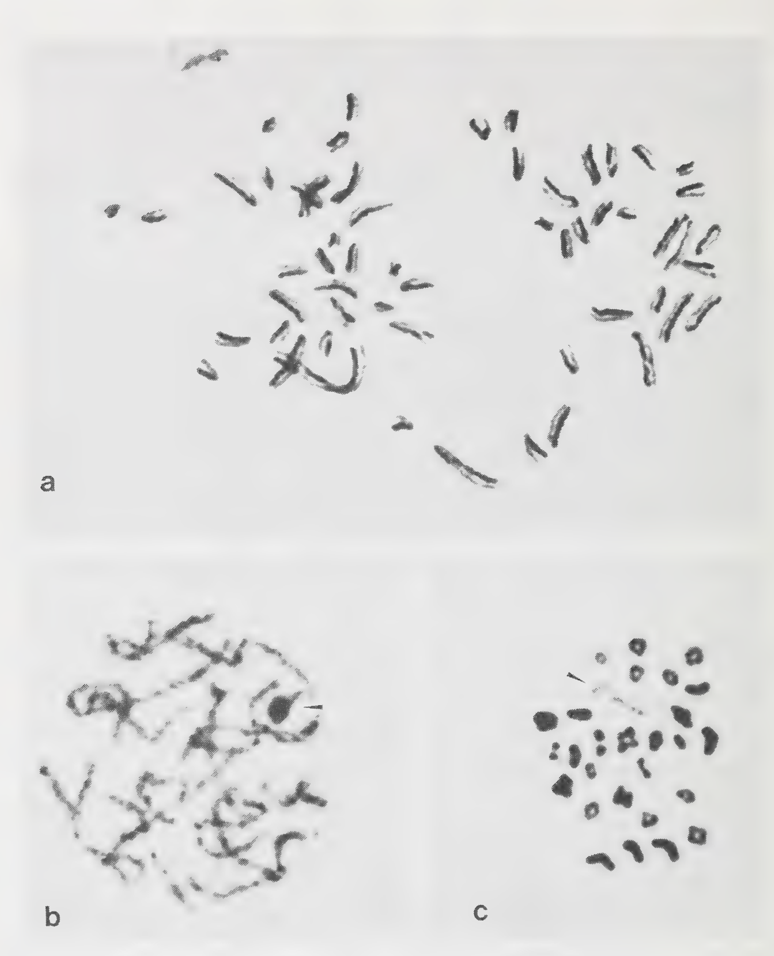
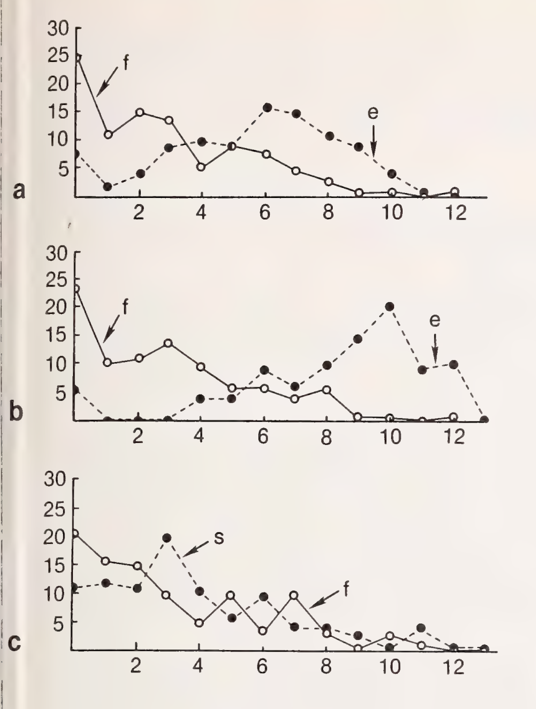


Fig. 3. a: Metaphase cell of *C. rutilus* after BrdU incorporation and modified FPG staining. An unusually large number of sister chromatid exchanges (eleven) may be noted. b: Giemsa stained pachytene cell from a male *C. californicus*, with the arrowhead pointing out the sex vesicle; c: Giemsa stained diakinesis cell from a male *C. californicus* with the arrowhead indicating the free end of the X



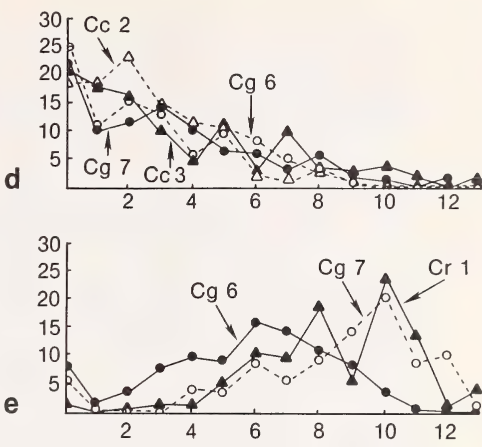


Fig. 4. Distributions of Ag-NORs in five different comparisons. Abscissa indicates the number of Ag-NORs per cell and the ordinate the number of cells (%). a: *C. gapperi* 6 femur bone marrow (abbrev. f) and ear fibroblast (abbrev. e) cells; b: *C. gapperi* 7 femur bone marrow and ear fibroblast cells; c: *C. californicus* 3 femur bone marrow and spleen (abbrev. s) cells; d: Femur bone marrow cells from *C. gapperi (Cg)* and *C. californicus (Cc)*; e: Fibroblast cells from *C. gapperi (Cg)* and *C. rutilus (Cr)*

Discussion

G-banding, C-banding and systematic relationships

The comparative cytogenetic data for the genus *Clethrionomys* derived both from the present study and from the literature may be summarized with respect to intraspecific and interspecific variability. Six species have been karyotypically examined, the five discussed here and *C. andersoni* (Obara 1986). All six species have 2n = 56 and NF_a = 56, with the exception of a specimen of *C. rutilus* from Alaska that was heterozygous for a centric fusion and thus had 2n = 55 (Rausch and Rausch 1975). Populations of *C. gapperi* from Vermont, Virginia and West Virginia (Modi 1987a, b; present study), Wisconsin, and Wyoming (Nadler et al. 1976) have now been examined using chromosomal banding procedures. With the exception of the two autosomal C-band heteromorphisms reported here in the male specimen from West Virginia, no intraspecific variability has been noted, although it is difficult to accurately compare our preparations with those of Nadler et al. (1976). Differences in the amount of pericentromeric autosomal C-bands were observed among individuals of *C. glareolus* from Austria and France (Gamperl 1982a). Nadler et al. (1976) suggested minor differences in G-banding patterns may exist among Soviet and Alaskan samples of *C. rutilus*. Finally, G-banding patterns between *C. rufocanus* from Japan (Mascarello et al. 1974) and Sweden (Gamperl 1982a) appear identical.

Three of these six species are known to exhibit intraspecific variability in Y chromosome size and/or morphology. Medium-sized acrocentric or metacentric elements are known in different populations of *C. rutilus* and *C. rufocanus* (Vorontsov et al. 1978), while acrocentric, metacentric (Král 1972; Vorontsov et al. 1978), and submetacentric (Gamperl 1982a) elements exist among *C. glareolus*. On the other hand, intraspecific Y chromosome variability has not yet been reported for the three remaining species. Among

these, the Y in *C. californicus* is an extremely small-sized acrocentric (Modi 1985), while in *C. gapperi* and *C. andersoni* the element is a medium-sized acrocentric. Modi (1987b) has argued that a medium-sized acrocentric, C-band positive element is the primitive Y chromosome among species in the family Arvicolidae. If this is correct, then derived Y chromosomes are present among populations of four of the six species thus far karyotypically examined.

Interspecific comparisons of G-banded karyotypes indicate that *C. rufocanus* and *C. andersoni* have identical karyotypes, although minor differences in staining intensity exist among several pairs of autosomes (Obara 1986). These two species differ from the remaining four studied here due to the presence of the 1/9 reciprocal translocation. As suggested earlier (Gamperl 1982a) and supported elsewhere (Modi 1987a), based upon outgroup comparisons with G-banded chromosomes from other arvicolid and cricetid rodent species, the constitution of chromosomes 1 and 9 as found in *C. rufocanus* and *C. andersoni* is regarded as primitive, while the arrangement found in the other four species is derived.

The isolated systematic position of *C. rufocanus* and *C. andersoni* relative to the related *C. rutilus, C. glareolus, C. californicus* and *C. gapperi* as suggested by the 1/9 translocation is supported by several other studies. Traditional morphological comparisons assign *C. rufocanus* to a monotypic subgenus (Miller 1900). Additionally, Corbet (1978) and Obara (1986) feel that *C. rufocanus* and *C. andersoni* are more closely related to one another than to any other living forms. Viable F_1 hybrid offspring have been produced in laboratory breeding studies between *C. glareolus* and *C. gapperi* (Grant 1974), and between *C. glareolus* and *C. rutilus* (Spannhof 1960; Rauschert 1963; Zimmermann 1965); while attempted crosses between *C. rutilus* and *C. gapperi* have been unsuccessful (Matthey 1953; Zimmermann 1965). Nadler et al. (1976) have suggested that *C. rutilus* may be a derivative of *C. glareolus* and that an ancestral *glareolus-gapperi*-like form may have had a trans-Beringian mid-Pleistocene distribution. They also point out that *C. rufocanus* and *C. rutilus* are well differentiated morphologically from one another throughout most of their considerably overlapping geographic distributions. Based upon protein electrophoresis Graf (1982) found *C. rufocanus* and *C. glareolus* to be more closely related to species belonging to other genera of arvicolids than to one another. Using DNA-DNA solution hybridization, Catzeflis et al. (1987) studied eight species of arvicolids including three species of *Clethrionomys*. They found the species of *Clethrionomys* to be much more closely related to one another than to species of *Microtus, Arvicola* or *Lemmus,* with *C. glareolus* and *C. gapperi* being slightly more similar to one another than either was to *C. rutilus*. Finally, Tegelström (1987) interpreted information derived from mitochondrial DNA restriction endonuclease digestion patterns as evidence for the occurrence of a limited episode of interspecific hybridization between natural populations of *C. glareolus* and *C. rutilus* in Fennoscandia.

The extreme interspecific chromosomal conservatism found here among *Clethrionomys* (only one major interspecific karyotypic difference) is in marked contrast to the patterns seen in other genera of arvicolid rodents such as *Microtus* (Gamperl 1982b, 1982c; Modi 1987a) *Dicrostonyx* (Gileva 1983) and *Ellobius* (Lyapunova et al. 1980). In these genera, interspecific karyotypic differences are often pronounced and attributable to one or more structural rearrangements. For example, Modi (1987a) analyzed G-banded karyotypes for 22 species belonging to eight genera and found a total of 141 euchromatic rearrangements accounting for the extensive interspecific chromosomal variation. The striking homogeneity found in *Clethrionomys* resembles the situation seen among vespertilionid bats of the genus *Myotis* (Bickham et al. 1986), the cat family (Wurster-Hill and Centerwall 1982), and seals (Arnason 1977). Although several factors, such as mutation rates, effective population sizes, fecundity effects due to chromosome segregational behavior at meiosis, and the phenotypic effects of novel homokaryotypes or heterokaryo-

types are thought to be responsible for the origination and fixation of chromosomal rearrangements (WHITE 1978), there is no empirical support indicating why a group such as *Clethrionomys* should be nearly chromosomally invariant while other related groups exhibit extensive interspecific karyotypic variation. From this, it appears that structural chromosomal differences are not a prerequisite for the attainment of reproductive isolation among *Clethrionomys*.

Silver-staining and rDNA transcriptional activity

It is generally accepted that silver positive staining of nucleolus organizer regions in metaphase chromosomes is indicative of rDNA gene activity (MILLER et al. 1976). Results of the present study are interpreted with respect to tissue, individual and species specific differences in rDNA gene expression as evidenced by the silver staining technique.

Significantly greater mean numbers of Ag-NORs were seen in fibroblast cells than in femur bone marrow cells in both specimens of *C. gapperi*, whereas a significant difference was not seen between the femur and spleen tissues in the single specimen of *C. californicus*. This indicates greater rDNA transcriptional activity in cultured cells than in noncultured cells from the same individual, but similar levels of transcriptional activity among the two noncultured tissue types within an individual.

Various results from other studies have been reported regarding intraindividual tissue specific silver staining properties of NORs. Human bone marrow cells have fewer Ag-NORs and demonstrate greater intercellular heterogeneity in silver staining than do cells derived from other tissues (REEVES et al. 1982; MAMAEV et al. 1985). Similarly, MERRY et al. (1983) found tissue specific differences among the opossums they examined. The basis for tissue specific differences in rDNA transcriptional activity is not understood. However, this variability may be attributable to differential maturation rates of bone marrow cells (MAMAEV et al. 1985), differences in cell cycle times or metabolic requirements of the tissues, differential cell growth and/or variation in the availability of necessary transcriptional control factors.

The other two comparisons that were carried out (analyzing similar tissues between individuals of different species) indicated that individual differences in silver staining do exist and that specimens of one species may be more similar to individuals of other species than to other conspecifics. This suggests that intraspecific variability in silver staining is equal to or greater than interspecific differences among *Clethrionomys*, and thus this type of comparison is of limited taxonomic utility.

Sister chromatid exchange

Sister chromatid exchange (SCE) represents recombination of DNA at apparently homologous loci, with such exchange occurring seemingly at random throughout the genome. Although the basis for SCE is not known, the procedure has been widely used as a measure of mutagenicity and genotoxicity (LATT et al. 1979). The two procedures generally used for SCE detection (autoradiography using tritiated thymidine and BrdU incorporation) are both known to increase the frequency of SCE. This observation has led to the question of whether or not SCE occurs spontaneously in living cells. A number of studies has addressed this issue by measuring SCE both in vitro and in vivo by administering various concentrations of BrdU, calculating dose-response curves and extrapolating from a linear region of the curve to predict what the SCE frequency would be in the absence of BrdU. Recently, TUCKER et al. (1986) measured SCE frequencies in human and mouse peripheral lymphocytes using monoclonal antibodies and very low (20–30 nM) concentrations of BrdU, and predicted spontaneous frequencies of 7.2 SCE/cell and 4.8 SCE/cell for the two species, respectively.

A dose response curve was not generated in the present study for *C. rutilus* rather a SCE frequency of 8.0 per cell was determined at a single BrdU concentration of 30 μg/ml. By comparing this result to the curves presented in other studies and interpolating at similar BrdU concentrations, the frequency found here in lung fibroblast cells of *C. rutilus* is consistent with the findings reported for a Chinese hamster fibroblast cell line where a frequency of about 7.5 exchanges per cell was reported (Kato 1974). On the other hand, Kram (1979) reported higher SCE frequencies of about 20 per cell in mouse fibroblast cells.

Meiotic analyses

The presence of a sex vesicle in meiotic pachytene cells has been observed for a number of mammalian species. This structure is thought to function as a means of keeping the X and Y chromosomes in association, since they share limited DNA sequence homology and typically synapse less extensively than do autosomal bivalents. Generally, the sex chromosomes then assume an end-to-end association as the meiotic cycle progresses into diakinesis (Solari 1974).

A conventional sex vesicle and end-to-end association were observed here in the preparations from *C. californicus*. It appears as though the centromeric end of the X synapses with the small-sized Y chromosome in this species. Similar association of the centromeric region of an acrocentric X with the Y was reported in a South American cricetid rodent (Sbalqueiro et al. 1984), while in the mouse *(Mus musculus)* the telomeric region of the acrocentric X pairs with the Y (Hsu et al. 1971). If this synapsis is due to the presence of homologous pseudoautosomal DNA sequences on the sex chromosomes (Pritchard and Goodfellow 1985), then it would appear that these sequences are located at a different chromosomal region of the mouse X compared with the location of the sequences in these two other rodent species. Further, the extreme small size and C-band negative staining property of the Y in *C. californicus* may be the result of o loss of highly repetitive DNA sequences, while the pseudoautosomal sequences and those involved with testis determination and male fertility have been retained.

Acknowledgements

M. R. Lee provided technical assistance, C. W. Kilpatrick made available specimens of *C. gapperi* from Vermont, and G. Jarrell provided the *C. rutilus*. O. Kepka, A. Meylan, and R. Schröpfer made available specimens of *C. glareolus* and *C. rufocanus*.

Research sponsored, at least in part, by the National Cancer Institute, DHHS, under contract NO1-CO-74102 with Program Resources, Incorporated. The contents of this publication do not necessarily reflect the views or policies of the DHHS, nor does mention of trade names, commercial products, or organizations imply endorsement by the U.S. Government.

Zusammenfassung

Vergleich chromosomaler Bändermuster von amerikanischen und europäischen Rötelmäusen, Gattung Clethrionomys

G-Bänder von Chromosomen folgender fünf *Clethrionomys*-Arten werden beschrieben: *C. glareolus, C. rufocanus, C. gapperi, C. californicus* und *C. rutilus*. Entsprechende Daten stehen auch noch für eine weitere Art, *C. andersoni,* aus der Literatur zur Verfügung. *C. glareolus, C. gapperi, C. californicus* und *C. rutilus* sind durch eine abgeleitete reziproke Translokation eines Autosomenpaares gekennzeichnet, während in *C. rufocanus* und *C. andersoni* der primitive Zustand erhalten geblieben ist. Die Variabilität der C-Bänder ist sowohl zwischen als auch innerhalb der Arten sehr gering. Konvergente Variationen hinsichtlich Form und Länge des Y-Chromosoms kommen bei drei Arten vor. Chromosomale Unterschiede zwischen verschiedenen Arten der Gattung *Clethrionomys* sind wesentlich geringer als in anderen Wühlmaus-Gattungen, d. h. die Evolution in *Clethrionomys* hat stattgefunden ohne gleichzeitige Chromosomenveränderungen. Die Aktivität der ribosomalen DNA (rDNA) wurde in fünf verschiedenen Gewebearten von Individuen dreier Arten mit Hilfe der

Silberfärbung (NOR-Färbung) untersucht. Dabei ergab sich, daß Fibroblasten eine wesentlich höhere Anzahl von Nukleolusorganisatorregionen (Ag-NOR's) aufweisen als Knochenmarkszellen desselben Tieres. Die intraspezifische Variabilität der Zahl von NOR's pro Zelle innerhalb eines bestimmten Gewebes ist gleich oder größer als Unterschiede zwischen verschiedenen Arten. Die Häufigkeit von Schwesterchromatidaustauschen (SCE's) wurde nach Einbau von 5-Bromdeoxiuridin (BrdU) in einer Zellinie aus Lungenfibroblasten von *C. rutilus* bestimmt. Die durchschnittliche Zahl der SCE's pro Zelle beträgt 8,0 und ist damit gleich hoch bzw. etwas niedriger als bei anderen Nagerarten. Untersuchungen der Meiose von *C. californicus* zeigten, daß zwischen der Zentromerenregion des X-Chromosoms und dem sehr kleinen, C-Band-negativen Y-Chromosom eine End-zu-End-Assoziation in der Diakinese besteht.

Literature

Arnason, Ú. (1977): The relationship between the four principle pinniped karyotypes. Hereditas **87,** 227–242.

Bickham, J. W.; McBee, K.; Schlitter, D. A. (1986): Chromosomal variation among seven species of *Myotis* (Chiroptera: Vespertilionidae). J. Mammalogy **67,** 746–750.

Bloom, S. E.; Goodpasture, C. (1976): An improved technique for selective silver staining of nucleolar organizer regions in human chromosomes. Hum. Genet. **34,** 199–206.

Catzeflis, F. M.; Sheldon, F. M.; Ahlquist, J. E.; Sibley, C. G. (1987): DNA-DNA hybridization evidence of the rapid rate of muroid rodent evolution. Mol. Biol. Evol. **4,** 242–253.

Corbet, G. B. (1978): The Mammals of the Palearctic Region: A Taxonomic Review (Brit. Mus. Nat. Hist. London).

Gamperl, R. (1982a): Chromosomal evolution in the genus *Clethrionomys.* Genetica **57,** 193–197.

— (1982b): Tandam-Fusion als chromosomaler Evolutionsmechanimus bei *Microtus agrestis* (Rodentia, Microtinae). Z. Säugetierkunde **47,** 317–320.

— (1982c): Die Chromosomen von *Microtus arvalis* (Rodentia, Microtinae). Z. Säugetierkunde **47,** 356–363.

Gileva, E. A. (1983): A contrasted pattern of chromosome evolution in two genera of lemmings, *Lemmus* and *Dicrostonyx* (Mammalian, Rodentia). Genetica **60,** 173–179.

Graf, J.-D. (1982): Génétique biochemique, taxonomie et évolution des Arvicolidae (Mammalia, Rodentia). Rev. suisse. Zool. **89,** 749–787.

Grant, P. R. (1974): Reproductive compatibility of voles from separate continents (Mammalia: *Clethrionomys*). J. Zool. London **174,** 245–254.

Honacki, J. H.; Kinman, K. E.; Koeppl, J. W. (1982): Mammal species of the world. Allen Press and Association of Systematic Collections: Lawrence Kansas.

Hsu, T. C.; Arrighi, F. E. (1971): Distribution of constitutive heterochromatin in mammalian chromosomes. Chromosoma **34,** 243–253.

Kato, H. (1974): Spontaneous sister chromatid exchanges detected by a BudR-labelling method. Nature **251,** 70–72.

Král, B. (1972): Chromosome characteristics of Muridae and Microtinae from Czechoslovakia. Act. Sci. Nat. (Brno) **6,** 1–18.

Kram, D.; Schneider, E. L.; Senula, G. C.; Nakanishi, Y. (1979): Spontaneous and mitomycin-c induced sister chromatic exchanges: comparisons of in vivo and in vitro systems. Mut. Res. **60,** 339–347.

Latt, S. A.; Allen, J. W.; Rogers, W. E.; Jeurgens, L. A. (1979): In vitro and in vivo analysis of sister chromatid exchange formation. In: Handbook of mutagenicity test procedures. Ed by B. J. Kilbey, M. Legator, W. Nichols and C. Ramel. Amsterdam: Elsevier Press. Pp. 275–292.

Lee, M. R.; Elder, F. F. B. (1980): Yeast stimulation of bone marrow mitosis for cytogenetic investigations. Cytogenet. Cell. Genet. **26,** 36–40.

Lyapunova, E. A.; Vorontsov, N. N.; Korobitsyna, K. V.; Ivanitskaya, E. Yu; Borisov, Yu M.; Yakimenko, L. V.; Dovgal, V. Ye (1980): A Robertsonian fan in *Ellobius talpinus.* Genetica **52/53,** 239–247.

Mamaev, N.; Mamaev, S.; Liburkina, I.; Kozlova, T.; Medvedova, N.; Makarkina, G. (1985): The activity of nucleolar organizer regions of human bone marrow cells studied with silver staining. I. Chronic myelocytic leukemia. Cancer Genet. Cytogenet. **16,** 311–320.

Mascarello, J. T.; Stock, A. D.; Pathak, S. (1974): Conservatism in the arrangement of genetic material in rodents. J. Mammalogy **55,** 695–704.

Matthey, R. (1953): Les chromosomes des Muridae. Rev. Suisse Zool. **60,** 225–283.

Merry, D. E.; Pathak, S.; Vande Berg, J. L. (1983): Differential NOR activities in somatic and germ cells of *Monodelphis domestica* (Marsupialia, Mammalia). Cytogenet. Cell Genet. **35,** 244–251.

Miller, D. A.; Dev, V. G.; Tanthravahi, R.; Miller, O. J. (1976): Suppression of human nucleolus organizer activity in mouse human somatic cell hybrids. Exp. Cell Res. **101,** 235–243.

Miller, G. S. (1900): Preliminary revision of the European redbacked mice. Proc. Wash. Acad. Sci. **11**, 83–109.
Modi, W. S. (1985): Chromosomes of six species of New World microtine rodents. Mammalia **49**, 357–363.
— (1987a): Phylogenetic analyses of chromosomal banding patterns among the Nearctic Arvicolidae (Mammalia: Rodentia). Syst. Zool. **36**, 109–136.
— (1987b): C-banding analyses and the evolution of heterochromatin among arvicolid rodents. J. Mammalogy **68**, 704–714.
Nadler, C. F.; Rausch, V. R.; Lyapunova, E. A.; Hoffmann, R. S.; Vorontsov, N. N. (1976): Chromosomal banding patterns of the Holarctic rodents, *Clethrionomys rutilus* and *Microtus oeconomus*. Z. Säugetierkunde **41**, 137–146.
Obara, Y. (1986): G-band homology between the Japanese red-backed vole, *Clethrionomys a. andersoni* and the grey red-backed vole, *C. rufocanus*. Chrom. Info. Serv. **40**, 7–9.
Perry, P.; Wolff, S. (1974): New Giemsa method for the differential staining of sister chromatids. Nature **251**, 256–258.
Pritchard, C.; Goodfellow, P. N. (1985): The pseudoautosomal region and telomeres: the beginning of the end? Trends Genet. **1**, 289–290.
Rauchert, K. (1963): Sexuelle Affinität zwischen Arten und Unterarten von Rötelmäusen *(Clethrionomys)*. Biol. Zentralbl. **82**, 653–664.
Rausch, R. L.; Rausch, V. R. (1975): Relationships of the red-backed vole, *Clethrionomys rutilus* (Pallas), in North America: karyotypes of the subspecies *dowsoni* and *albiventer*. Syst. Zool. **24**, 163–170.
Reeves, B. R.; Casey, G.; Harris, H. (1982): Variations in the activity of nucleolus organizer regions in different tissues, demonstrated by silver staining of human normal and leukemic cells. Cancer Genet Cytogenet **6**, 223–230.
Sbalqueiro, I. J.; Mattevi, M. S.; Oliveria L. F. B. (1984): An $X_1X_1X_2X_2/X_1X_2Y$ mechanism of sex determination in a South American rodent, *Deltamys kempi* (Rodentia, Cricetidae). Cytogenet. Cell Genet. **38**, 50–55.
Seabright, M. (1971): A rapid banding technique for human chromosomes. Lancet **ii**, 971–972.
Solari, A. J. (1974): The behavior of the XY pair in mammals. Int. Rev. Cytol. **38**, 273–317.
Spannhof, L. (1960): Histochemische Untersuchungen zur Sterilität bei männlichen Säugerbastarden (Artkreuzung der Rötelmäuse *Clethrionomys glareolus* x *Cl. rutilus*). Verhdl. Dt. Zool. Ges., Zool. Anz., Suppl. **23**, 99–107.
Sumner, A. T.; Evans, H. J.; Buckland, R. (1971): New technique for distinguishing between human chromosomes. Nature New Biol. **232**, 31–32.
Sumner, A. T. (1972): A simple technique for demonstrating centromeric heterochromatin. Expl. Cell. Res. **75**, 304–306.
Tegelström, H. (1987): Transfer of mitochondrial DNA from the northern red-backed vole *(Clethrionomys rutilus)* to the bank vole *(C. glareolus)*. J. Mol. Evol. **24**, 218–227.
Tucker, J. D.; Christensen, M. L.; Strout, C. L.; Carrano, A. V. (1986): Determination of the baseline sister chromatid exchange frequency in human and mouse peripheral lymphocytes using monoclonal antibodies and very low doses of bromodeoxyuridine. Cytogenet. Cell. Genet. **43**, 38–42.
Vorontsov, N. N.; Lyapunova, E. A.; Ivanitskaya, E. Yu; Nadler, C. F.; Král, B.; Kozlovsky, A. I.; Hoffmann, R. S. (1978): Variability of sex chromosomes in mammals. I. Geographical variability of morphology of Y-Chromosome in genera *Clethrionomys* (Rodentia, Microtinae). Genetika **14**, 1432–1446 (in Russian).
White, M. J. D. (1978): Modes of speciation. San Francisco: W. H. Freeman.
Wurster-Hill, D. H.; Centerwall, W. R. (1982): The interrelationships of chromosome banding patterns in canids, mustelids, hyena, and felids. Cytogenet. Cell Genet. **34**, 178–192.
Zimmermann, K. (1965): Art-Hybriden bei Rötelmäusen. Z. Säugetierkunde **30**, 315–320.

Authors' addresses: Dr. William S. Modi, Biological Carcinogenesis Development Program, Program Resources, Inc., Frederick Cancer Research Facility, P.O. Box B, Frederick, MD 21701, U.S.A., and Dr. Roswitha Gamperl, Institut für Medizinische Biologie und Humangenetik, Universität Graz, Harrachgasse 21/8, A-8010 Graz, Austria

Z. Säugetierkunde 54 (1989) 153–156

ISSN 0044-3468

Natural History Museum of Slovenia, Ljubljana, and Department of Zoology, University of Zagreb, Yugoslavia

Vertical distribution of the Snow vole *Microtus nivalis* (Martins, 1842) in Northwestern Yugoslavia

By B. Kryštufek and D. Kovačić

Receipt of Ms. 20. 2. 1987

Abstract

Studied the vertical distribution of snow vole in Northwestern Yugoslavia. The distribution of localities ranges between 30 and 2450 m above sea level. 43 % out of 37 localities are below 1000 m and 11 % are below 100 m. It is suggested that the snow vole distribution is affected by the presence of deep fissures with stable cavernicolous conditions in the stony habitat and not by altitude.

Introduction

The vertical distribution of the snow vole *Microtus nivalis* (Martins, 1842) is between 100 and 4700 m above sea level in Europe (Krapp 1982) while the best living conditions, at least in the Alps, are above 1000 m (Clouarn and Janeau 1975). Localities below 1000 m, lying between 100 and 600 m have been reported from Spain, France, Italy, Yugoslavia, Greece and Bulgaria (Krapp 1982). The lowest locality is apparently Latour-de-France, where snow vole remains were found in Barn owl *(Tyto alba)* pellets at about 100 m (Fons and Libois 1977). Four localities from the lowlands of Western Yugoslavia were reported by Jones and Carter (1980). The snow vole inhabits stony places above the tree line and is absent from the forests in the Alps (Kahmann and Halbgewachs 1962; Louarn and Janeau 1975) in the Carpathians (Kowalski 1957) and in the Tatras (Kratochvil 1981).

Recently, a large number of sites of the snow vole have been found below 1000 m in Northwestern Yugoslavia. The objective of this paper is to describe the vertical distribution of the species in the studied area, to analyse the causes which condition it and, by doing so, to construct a hypothesis to explain its vertical distribution in general.

Material and methods

The original data were collected by snap trapping and analysis of owl pellets (the latter are marked by an asterix in the list of localities). All available data on the snow vole in Northwestern Yugoslavia, north of latitude 45 ° were used, as well as some data from the Italian border area.

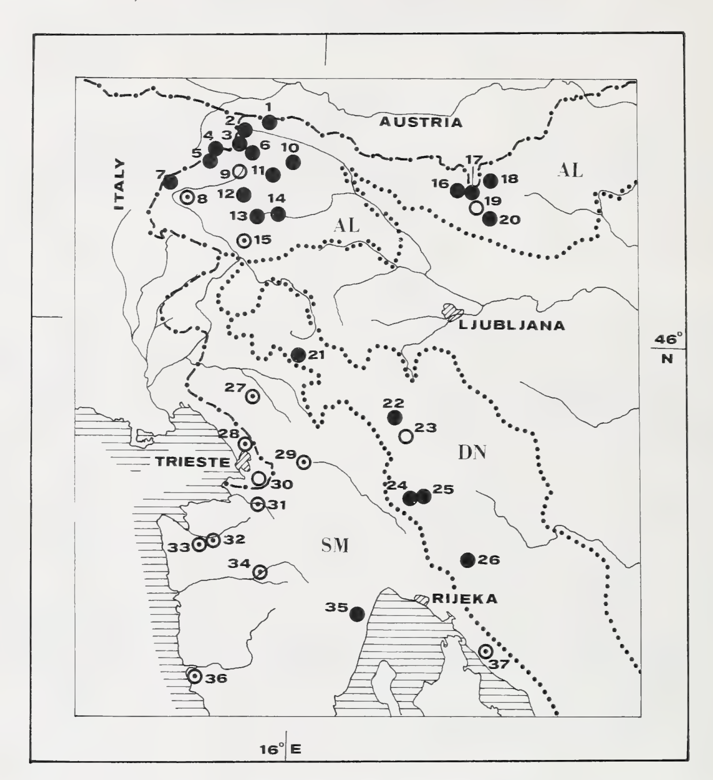
Results

The snow vole has been found in 37 localities: 20 in the Alps, 6 in the Dinarids (Dinaric Alps) and 11 in the Submediterranean region.

List of localities (Fig. 1):
1. Za Lepim vrhom, 1200 m; 2. Planica, 1000 m; 3. Tamar, 1200 m; 4. Mangart, 1900–2050 m; 5. Mangartska planina, 1300 m; 6. Vršič, 2000 m (Petrov 1968); 7. Kanin, Koča Peter Skalar, 1810 m; Kanin, Prestrelnik, 2050 m (Leg.: S. Brelih); 8. Log Čezsoški, 470 m (Leg.: J. Gregori and S. Brelih);

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5403-0153 $ 02.50/0

9. Trenta, Na Logu, 620 m (Leg.: S. Brelih); 10. Zgornja Krma, 1750 m (V. and E. MARTINO 1940); Krma, 1000–1100 m (PETROV in litt.); 11. Triglav, Ivačičeva jama, 2450 m (NOVAK and KUŠTOR 1983); 12. Krnsko jezero, 1400 m; 13. Bogatinsko sedlo, 1800 m; 14. Rodica (PETROV, in litt.); 15. Pološka jama, 440 m; 16. Zeleniške špice, Kamniška jama; 17. Kamniško sedlo, 1550–1600 m (Leg.: S. Brelih); 18. Štruca, Skuta, 2450 m; 19. Kamniška Bistrica, 600–900 m; Velika planina, 1665 m; 21. Čaven, 1100–1200 m (PETROV, in litt.); 22. Javornik, 1100 m (Leg.: S. Brelih); 23. Cerkniško jezero, Otok, 550 m (PETROV, in litt.); 24. Snežnik, Svinščaki, 1240 m; Snežnik, 1600–1700 m; 26. Risnjak, 1450–1500 m; 27. San Daniele (= Štanjel), approx. 365 m (DAL PIAZ 1927); 28. Padriciano, 360 m (LAPINI 1984); 29. Divača, Škocjanske jame, 325 m; 30. Banjoli, 100 m; 31. Osp, 50 m (Leg.: J. Gregori and S. Brelih); 32. ★ Buje, Momjan, 320 m; 33. ★ Sinkovići; 34. Istarske toplice, 30 m; 35. Učka, 1000 m (PETROV 1968); 36. ★ Rovinj, approx, 35 m; 37. Crikvenica, 1.5 km N, 3 km E, 300 m (JONES and CARTER 1980).



Map of localities in Northwestern Yugoslavia where the snow vole has been found. Closed circles – localities above 1000 m above sea level; open circles – localities between 100 and 1000 m; open circles with dot – localities at 100 m and below. The dotted line separates the regions (according to WRABER 1969): AL – Alpine; DN – Dinaric; SM – Submediterranean

The vertical distribution of the snow vole is between 30 and 2450 m. 4 of the 20 Alpine localities were between 440 and 1000 m and the remaining 16 were above 1000 m. All finds were from open habitats, mainly in the mountain grassland belt and the mountain pine *(Pinus mugo)* belt. In the belt of beech-wood forest *(Anemone-Fagetum)*, the snow vole is confined to bare stone cliffs, dry torrential canyons, and on scree slopes. No findings of the snow vole were recorded in dense forest.

Any suitable habitats above 550 m could be inhabited by the snow vole in the Dinarids. The upper limit of its distribution is determined by the height of the heighest peaks. The snow vole was most widely distributed in the region of mountain pine forest. It was also

found in the mature forests of *Fagetum subalpinum* and *Abieti-Fagetum illyricum*, where it was limited to large accumulations of stones, sinkholes and fissures connected to caves.

The snow vole was found between 30 and 1000 m in the Submediterranean. With the exception of Učka (1000 m) all localities were below 500 m. The lowest four localities are below 100 m. All the animals were caught to or within fissures in the limestone. The snow vole enters underground caves (point 29 in Fig. 1), and inhabits steep, bare, Karst cliffs (31), quarries (34) and river canyons (30).

Discussion

The snow vole is mainly reported to live on open mountain slopes above the tree line (Corbet and Ovenden 1980). Its appearance in low altitudes is regarded as an anomally (Miller 1912) or at least a rarity. Very few attempts have so far been made to connect actual distribution with other peculiarities of its life (e. g. Tvrtković 1976). The snow vole is morphologically adapted to a petricolic way of life (Ognev 1950; Kratochvil 1956; Krapp 1982). It inhabits fissures typical of stony habitats in which cavernicolous conditions can be expected. We assume that the stable, mainly stenothermal conditions in the (micro) cavernicolous habitat are the main factor determaining its distribution. The snow vole is thus considered to be a troglophilic animal.

The temperature of a cavernicolous habitat is equal to the average yearly temperature of the region. In the studied area, the average ground temperature is +13,1 °C at the coast (Rovinj, 5 m), +5 °C in the Dinarids (Mašun at Snežnik Mt., 1017 m), and −1.6 °C in the Alps (Kredarica, 2514 m). The ground temperature of the Alpine ice cave near Kredarica (alt. 2450 m), which is inhabited by the snow vole, was found to be between +2.4 and −5.5 °C, measured at 28 sites throughout the year. In many places, the temperature did not fall below 0 °C (Novak and Kuštor 1983). One would not expect the snow vole to need any special adaptation to extremely low temperatures. Bienkowski and Marszalek (1974) demonstrated that the metabolism of the snow vole does not differ from that of the bank vole *(Clethrionomys glareolus)*. They presumed that the snow vole is a high mountain species, so the similarity between the snow vole and the bank vole was explained by the hypothetical mountainous origin of the latter. Some peculiarities of the snow vole metabolism, its heterothermia and almost identical energy budgets for winter and summer (Bienkowski and Marszalek 1974) indicate a species adapted to stable conditions. Its attachment to the stenothermal habitats implies a relict species, which corresponds to its recent distribution area (Krapp 1982). We attribute the atachment of the snow vole to high mountain habitats in the Alps, Carpathians and Tatras to the lack of suitable cavernicolous habitats at lower altitudes, especially below 1000 m.

The situation is additionally complicated by the presence of another petricolic vole in the Balcan peninsula. Scramble competition between the snow vole and Martino's vole *(Dinaromys bogdanovi)* has a profound influence on their distribution. Martino's vole prevails over the snow vole in interspecific encounters (Petrov and Todorović 1982). The snow vole retreats to higher altitudes, which is most obvious in the Northern Velebit, where the Martino's vole inhabits localities from 400 to 900 m and the snow vole localities from 900 to 1700 m (Tvrtković 1984). In this and similar cases, the vertical distribution of the snow vole is a result of interspecific competition for habitat.

Acknowledgements

We are grateful to Dr. Boris M. Petrov (Belgrade) who has kindly allowed us to use his data on the snow vole in Northwestern Yugoslavia. We also thank him and Prof. Dr. Beatrica Djulić (Zagreb) for reading the manuscript and for suggesting helpful revisions.

Zusammenfassung

Vertikale Verbreitung der Schneemaus Microtus nivalis (Martins, 1842) im nordwestlichen Jugoslawien

Die Höhenverbreitung der Schneemaus in Nordwest-Jugoslawien reicht von 30 bis 2450 m ü. M. Von den 37 Fundorten liegen 43 % unter 1000 m und 11 % unter 100 m. Damit scheint das Vorkommen der Schneemaus weniger durch die Höhe als durch spalten- und höhlenreiche Habitate bestimmt zu sein.

References

Bienkowski, P.; Marszalek, U. (1974): Metabolism and energy budget in the snow vole. Acta theriol. **19**, 55–67.

Corbet, G.; Ovenden, D. (1980): The mammals of Britain and Europe. London: Collins.

Dal Piaz, G. B. (1927): I mammiferi fossili e viventi delle Tre Venezie. Rodentia. Studi Trentini **10** (1), 89–134.

Fons, R.; Libois, R. (1977): Presence du campagnol des neiges *Microtus nivalis aquitanicus* Miller, 1908, dans les collines du Roussillon. Vie Milieu **27**, 279–282.

Jones, J. K.; Carter, D. C. (1980): The snow vole, *Microtus nivalis*, in the lowlands of Western Yugoslavia. J. Mammalogy **61** (3), 572.

Kahmann, H.; Halbgewachs, J. (1962): Beobachtungen an der Schneemaus, *Microtus nivalis* Martins, 1842, in den Bayerischen Alpen. Säugetierkdl. Mitt. **10**, 64–82.

Kowalski, K. (1957): *Microtus nivalis* (Martins, 1842) (Rodentia) in the Carpathians. Acta theriol. **1**, 159–182.

Krapp, F. (1982): *Microtus nivalis* (Martins, 1842) – Schneemaus. In: Handbuch der Säugetiere Europas. Ed. by J. Niethammer and F. Krapp. Wiesbaden: Adakem. Verlagsges. Vol. **2**, 261–283.

Kratochvil, J. (1956): Tatra-Schneemaus *Microtus (Chionomys) nivalis mirhanreini* (Schäfer, 1935). Prace Brnenske Zaklad Českoslov. Adad. Ved. **28**, 1–39.

– (1981): *Chionomys nivalis* (Arvicolidae, Rodentia). Acta Sc. Nat. Brno **15** (11), 1–62.

Lapini, L. (1984): Catalogo della collezione erpetologica del Museo Friulano di Storia naturale. Udine: Museo Friulano di Storia naturale, Vol. **30**.

Louarn, H. Le; Janeau, G. (1975): Repartition et biologie du campagnol des nieges *Microtus nivalis* dans la region de Briancon. Mammalia **39**, 589–604.

Martino, V.; Martino, E. (1940): Notes on five new mammals from Yugoslavia. Ann. and Mag. Nat. Hist., London **11** (5), 493–498.

Miller, G. S. (1912): Catalogue of the mammals of Western Europe. London: British Museum (Nat. Hist.).

Novak, T.; Kuštor, V. (1983): On the ecology of an apine ice cave. Mem. Biospel. **10**, 117–125.

Ognev, S. I. (1950): Zveri SSSR i priležaših stran. Moskva, Leningrad: Akad. nauk SSSR. Vol. **7**.

Petrov, B. (1968): Korrekturen und Bemerkungen zu den Verbreitungskarten im Van den Brink-'schen Buch „Die Säugetiere Europas" für das Territorium Jugoslawiens. Säugetierkdl. Mitt. **16** (1), 39–52.

Petrov, B.; Todorović, M. (1982): *Dinaromys bogdanovi* (V. et E. Martino, 1922) – Bergmaus. In: Handbuch der Säugetiere Europas. Ed. by J. Niethammer and F. Krapp. Wiesbaden: Akad. Verlagsges. Vol. **2**, 193–208.

Tvrtković, N. (1976): Gnawing mammals (Rodentia) at the entrance to Karst-underground. Speleolog, Zagreb **22/23**, 4–6.

– – (1984): Vertical distribution of amphibians, reptiles and mammals (Amphibia, Reptilia, Mammalia) on the northern part of Mt. Velebit (Croatia, Yugoslavia). Zbornik radova, 3. kongres ekologa Jugoslavije, Sarajevo. Vol. **2**, 403–407.

Wraber, M. (1969): Pflanzengeographische Stellung und Gliederung Sloweniens. Vegetatio **17**, 176–199.

Authors' addresses: Dr. Boris Kryštufek, Natural History Museum of Slovenia, Prešernova 20, YU-61000 Ljubljana; D. Kovačić, Department of Zoology, Faculty of Sciences, University of Zagreb, Roosveltov trg 6, YU-41001 Zagreb, Yugoslavia

Z. Säugetierkunde 54 (1989) 157–171

ISSN 0044-3468

The diet of polecats (*Mustela putorius* L.) in Switzerland

By D. Weber

Museum of Natural History, Basel, Switzerland

Receipt of Ms. 23. 9. 1987

Abstract

Studied the diet of polecats in Switzerland by gut-analysis of 120 individuals and by analysis of 354 scats from 12 radiotracked individuals. Carcasses were collected from 1982 to 1987 from all over Switzerland and adjoining areas of France. Scats originate from a mountainous (1000–1300 m) and a lowland (300–450 m) study area. Results are given as weighted frequencies of occurrence, disregarding items of less than 25 % estimated sample volume.

The diet of polecats is almost exclusively carnivorous. Some fruits are also taken, mainly by juveniles. 43 animal species, 8 plant species, offal and pet food occurred as polecat food. Anurans (mainly *Rana temporaria* and *Bufo bufo*) are the staple food. Further elements of importance are small mammals (mainly Muridae, but also Microtidae and Soricidae), carrion, and eggs. The annuran proportion of the diet is higher in summer than in winter and higher in the mountains than in the lowlands. In mountainous regions, anurans are also the most important food in winter. Juveniles eat more fruits and invertebrates and fewer mammals than adults. Sex-related differences in the importance of the main food categories were not detected. Within the mammal and arthropod category, females showed a significant preference for larger prey.

Methods and results are discussed in various contexts. The diet of Swiss polecats differs strikingly by its high amphibian component from what has been published on the species until now. Possible reasons for this discrepancy are mentioned. The food niche of polecats overlaps only to a small extent with those of sympatric *Mustela erminea, Martes foina* and *M. martes*, which themselves show considerable niche overlap. The diet of polecats gives an additional argument in the debate on the origin of sexual dimorphism of mustelids.

Introduction

As elsewhere, polecat populations have declined in Switzerland during this century (Eiberle 1969; Mermod et al. 1983). In a thesis directed by Prof. U. Rahm at the Unsiversity of Basle, I tested several hypotheses which would explain this decline. One striking fact was the discription of the diet of polecats in literature, which is usually given as similar to that of stone martens *(Martes foina)*. Considering the decline of polecats and the recent increase of stonemarten populations in Switzerland (Müri 1982), this similarity suggested a food competition conflict as a possible reason for the decline of the polecat. On the other hand, if the increase of the stone marten was insufficient to explain the decrease of the polecat, why could other carnivores with similar diets increase their numbers, and not the polecat?

To answer these questions, it was necessary to obtain data on polecat diet in Switzerland, as all information on the subject came from countries with different ecological conditions. This paper presents the results of my study. I have discussed them in the context of the polecat decline elsewhere (Weber 1987). Here, they will be discussed in some contexts of more general interest.

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5403-0157 $ 02.50/0

Material and methods

Material and study areas

This study is based on scats and gut contents of polecats from Switzerland and adjoining areas of France.

The guts are from 84 carcasses, which I obtained from many sources (mainly taxidermists, gamekeepers and hunters). Additional 25 stomachs were made available by the Institute of Veterinary Bacteriology of the University of Berne and further 11 stomachs by the Veterinary Service Lons-le-Saunier, France. All animals died between the years 1982 and 1987. The causes of death were traffic (54), hunting (9), dogs (3), others (3) and unknown (51). The polecats were sexed and aged (mainly by means of cementum-annuli-counts, Weber 1987. Specimens which diet between June and November and were younger than one year are called juveniles in this paper; all others are called adults. Polecats from the Institute of Veterinary Bacteriology were aged and sexed by the staff of the institute. A list of the origin of all but five guts analysed for this paper is given in Weber (1987). In some cases, not all information about a carcass could be obtained.

The scats of radio-tracked polecats were collected at resting sites from 1983 to 1985 in two different areas (for a more extensive discription see Weber 1987): 1. Leimental (47° 30′ N, 7° 29′ E; altitude 300–450 m). A lowland valley with mainly arable farming and scattered deciduous forests of different areas. Many brooklets cross the area, which to the north-east, the city of basle, has an increasingly suburban character. The climate is warm compared to the rest of Switzerland, with mild winters (January mean 0 °C). In the Leimental area, 197 scats from 8 individuals were collected.

2. La Brévine mountains (46° 58′ N, 6° 39′ E; altitude 1000–1300 m). A chain of the Swiss Jura mountains south of La Brévine. About half the area consists of mountain mixed forests with *Picea abies* and *Abies alba* as dominant tree species. The rest is mainly covered with grassland and wooded pastures, which are structured by stone walls, hedges and combinations of both. There is virtually no surface water in this study area. Farmhouses and stables are isolated and scattered; only a fraction of them are used in winter. For the geographical latitude, the climate is cold with harsh and long winters and a vegetation period of approximately 140 days (January mean −4 °C, annual mean +4 °C). In the La Brévine area, 88 scats from 4 polecats were collected.

Snow-tracking provided some additional scats. In 5 cases, droppings were found scats stacked in "latrines". These heaps were frozen and cut into pieces of approximately 3 ml (the mean volume of 40 random-selected individual scats beeing 3.1 ml), trying to separate individual droppings as well as possible. By this procedure, I obtained 21, 10, 9, 8 and 6 samples, which are not identical with individual scats.

All faeces from radio-tracked polecats and most of those found on snow-tracks could be dated with an accuracy of a few days. However, for a pile of 71 scats from a stable in the La Brévine area this was not possible.

Treatment of the samples

The volume of the stomach contents was measured to the nearest ml. All samples were washed in a sieve (mesh width 0.8 mm). A second sieve (mesh width 0.14 mm) was used to retain potential earthworm chaetae and small molluscan radulae (Ashby and Elliot 1983). After the treatment of 354 scats the fine sieve was no longer used, as I found small numbers of chaetea in only 4 samples and no radulae. Washed prey remain types were macroscopically observed in suspension and, according to their visually estimated relative volume, assigned to one of the following categories: $>50\,\%$, $50\,\%$, $25\,\%$, $10\,\%$, $<10\,\%$.

For identification of hairs, medulla and scale patterns were observed microscopically and compared with the atlas of Debrot et al. (1982) and a collection of hairs of domestic mammals. Colour, macroscopical form or size also assisted identification in some cases. Mammals could often be identified by jaws or teeth according to Stresemann (1974) and Brohmer (1971). Amphibian bones were compared to reference skeletons. Where appropriate bones were found, species were identified according to Schaefer (1932). No attempts were made to identify fish remains. R. Winkler helped with the identification of some feathers. Other animal and fruit components could be attributed to species or higher taxonomic entities with the help of common field guides, reference collections and the personal experience of the author.

Three categories of prey remains are treated as carrion: 1. Animals which are too large to be killed by polecats (ungulates, dogs, cats, martens); 2. Animal remains which were found together with maggots; 3. Cases where radio-tracking revealed the food source (e.g. a polecat foraging on a rubbish-heap containing remains of slaughtered chickens). Some items were identified, but not considered as food remains (e.g. polecat hair, grass, dry leaves) and therefore not used to describe polecat diet.

The identification of prey remains was greately facilitated by the knowledge of the distribution of potential prey species in Switzerland, and especially in the radio-tracking study areas. This made it

possible to exclude for example wild rabbit and, depending on the sampling site, several anuran species as potential prey.

A fundamental problem arises from the presence of gut contents of prey animals in carnivore droppings and guts (ROSER and LAVERS 1976). I often found small, intact arthropods, which presumably originated from anuran stomachs: Of 79 samples with arthropods in small proportions ($\leq 10\%$ estimated volume), 78 contained also anuran bones. These 78 arthropod recordings are considered as anuran prey remains; a list of them is given in table 7.

Calculation of diet composition

Diet composition is given as relative frequency of occurrence (%) in the relevant sample. Every dropping, stomachal and intestinal content is thereby considered as an independent sample of a polecat meal. As most of the samples showed only one dominant prey type, this simple approach should give a representative image of food composition (DAY 1968).

To prevent the overestimating of mammals and birds (compared to amphibians), all prey forming an estimated 10 percent or less or remains in an individual sample, and all stomach contents with less than 1 ml, were not used to calculate diet composition. Thus, the analysis is restricted to items which form the bulk of individual samples; single hairs or feathers which can be found in a gut several days after ingestion of a mouse or a bird (ROSER and LAYERS 1976) were disregarded.

The distribution of remains used for frequency calculations over categories of estimated volume was as follows: >50 %: 467 identified prey types; 50 %: 64 i. p. t.; 25 %: 29 i. p. t. As frequencies are given as percentages of samples, remains in the 50 % category were scored as 0.5 and those in the 25 % category as 0.25 (ERLINGE 1981). The method underestimates the importance of eggs, meat from rubbish-heaps or pet food and other food with few undigestible components, when they occur together with other prey (BRUGGE 1977).

A food-niche breadth index was calculated according to Simpson's formula (MÜHLENBERG 1976): $N_B = 1/\Sigma\ p_i^2$. were p_i is the proportion of food category i in the diet. Niche breadth is therefore dependent on the number of defined food categories with values from 1 (only one category exploted) to i (all categories evenly exploited). In this paper, all niche breadth indices are based on the following 7 food categories: mammals, amphibians, other vertebrates, invertebrates, carrion/offal, eggs, fruits. This allows N_B values from 1 to 7.

When not specified, the statistical tests used are chi^2-tests (MÜHLENBERG 1976). Other tests were used according to SIEGEL (1956).

Results

Food components

In 34 of 120 stomachs no food remains were detected. A further 9 contained less than 1 ml and are also desregarded. In 11 of 83 intestines and 2 of 354 scats no food remains could be identified. A list of all individual samples including origin, place, date and main prey remains identified is given in WEBER (1987).

A list of all food items forming more than an estimated 10 % of the sample concerned is given in Tab. 1. As the samples are not randomly distributed over seasons, regions, age-groups or sexes, Tab. 1 does not give a representative figure of an average polecat diet in Switzerland. Therefore, no frequencies are given.

In the mammal group, most small ground-living species of the region are present. The considerable number of shrew records is remarkable. Ungulate and carnivore remains were interpreted as carrion. Remains of domestic rabbits were almost exclusively found in the droppings of a female polecat that foraged on a rubbish-heap with many carcasses available. Hare remains were once recorded together with several maggots. This item was considered as carrion. Having observed foraging polecats for several years, I believe that most of the hare records and all hedgehogs aught to be placed in this category. However, as I can not prove this, they have been retained in the "mammal" category for further analysis.

Chicken eggs are broken by feeding polecats and the contents are licked. Therefore, they often leave no traces in scats or intestines. Sometimes, when polecats had been observed while foraging, identification of bird species by fragments of eggshell was possible. The proportion of eggs in the polecat diet is certainly underestimated in this

Table 1. **Recorded food items of swiss polecats**

Food items		Rel. volume in sample >50 %	50 %	25 %
Mammalia	*Erinaceus europaeus*	1	1	–
Insectivora	*Sorex minutus*	1	–	–
	Sorex araneus	2	5	–
	Sorex/Neomys sp.	3	–	–
	Crocidura russula	3	–	–
	Crocidura sp.	3	–	–
	unid. Soricidae	1	–	–
	Talpa europaea	1	–	–
Lagomorpha	* *Oryctolagus cuniculus* f. dom.	10	3	–
	Lepus capensis	16	2	–
	* *Lepus capensis*	1	–	–
Rodentia	*Glis glis*	3	1	–
	Clethrionomys glareolus	8	3	–
	Arvicola terrestris	4	–	–
	Microtus arvalis	2	–	–
	Microtus agrestis	9	3	2
	Microtus/Pitymys sp.	10	3	1
	Ondatra zibethicus	1	1	–
	Apodemus sylvaticus	7	–	–
	Apodemus sp.	23	2	3
	Rattus norvegicus	11	4	1
	Mus musculus	3	–	–
	unid. Rodentia	1	–	–
Carnivora	* *Canis lupus* f. familiaris	1	–	–
	* *Martes martes*	2	–	–
	* *Felis sylvestris* f. catus	5	–	–
Artiodactyla	* *Sus scrofa*	1	–	–
	* *Capreolus capreolus*	3	1	–
	* *Capra aegagrus* f. hircus	5	–	–
Unid. Mammalia		–	1	–
Aves	*Gallus gallus* f. dom.	5	1	–
Eggs	*Meleagris gallopavo* f. dom.	1	–	–
	Gallus/Anas f. dom.	4	1	2
Wild birds	*Turdus viscivorus*	–	1	–
	Unid. Passeriformes	3	1	–
	Unid. Aves	4	2	–
Poultry	*Gallus gallus* f. dom.	5	1	1
	* *Gallus gallus* f. dom.	11	–	–
	Meleagris (?) f. dom.	1	–	–
Reptilia	*Lacerta agilis*	–	1	–
	Podarcis muralis	1	–	–
Amphibia	*Salamandra salamandra*	1	–	–
	Bufo bufo	135	9	4
	Rana "esculenta"	4	1	–
	Rana temporaria	39	2	1
	Rana sp.	43	6	5
	Unid. *Anura*	9	–	–
Pisces	Unid. fish	8	–	–
Invertebrata	*Arion* sp.	2	–	–
Mollusca	Tettigonioidea	1	–	1
Arthropoda	*Gryllotalpa gryllotalpa*	2	2	2
	Acridoidea	–	–	2
	Dermaptera	–	–	2
	Coleoptera	2	3	–
	Vespoidea	1	–	–
	Lepidoptera (mites)	–	2	–
	unid. Arthropoda	2	–	–

Table 1 (continued)

Food items		Rel. volume in sample		
		> 50 %	50 %	25 %
Annelida	Lumbricidae	–	–	2
Other Meat	Commercial catfood	1	–	–
	Meat/carrion	14	–	1
Plants	Apple	5	1	–
	Pear	1	–	–
	Plum	4	1	–
	Cherry	–	–	1
	Fig	1	–	–
	Tomato	2	–	–
	Unid. fruit	–	–	2
	Peanut	1	–	–
	Salad leaves	2	–	–

Items interpreted as carrion or offal are indicated with *. Not interpreted as food remains and therefore not included in this table: polecat hair, dirt, grass, hay, straw, tree-leaves, paper, rubber, trap-bait, tapeworms

paper. This can be illustrated by the following episode: One of the radiotracked polecats used a resting-site in a barn for two weeks. I collected there 6 droppings and the shells of 7 chicken eggs. None of these scats contained detectable egg remains. Similar observations were made several times.

11 scats with chicken remains (mainly skin from the legs and cervical vertebrae, no feathers) originate from a polecat who was observed taking offal behind a house. These samples will be considered as "carrion" in the following.

"*Rana esculenta*" is actually considered as two or three species, which were not distinguished appropriately in the identification key used. Most of the frogs mentioned as *Rana* sp. are probably *Rana temporaria*; other possible species (*R. lessonae, esculenta, ridibunda* and *dalmatina*) are rare or even absent in most of those areas from which samples originated.

No special attempts were made to identify fish and bird species, as these types of prey occurred only rarely. These animals are normally not hunted, but found as carrion (pers. observations). All in all, the "carrion/offal" category is surely underestimated in this paper, but not as extremely as the eggs.

Seasonal variations

Seasonal variation of diet composition is shown in fig. 1. In summer and autumn, amphibians (*Rana temporaria* and *Bufo bufo*) form the bulk of the food of Swiss polecats. Carrion/offal is of particular importance in winter, when the proportion of anurans is smaller. Considering the relative importance of these two food categories, I distinguish in the following the seasons "winter" (December to April) and "summer" (Mai to November).

The seasonal importance of food categories is given in tab. 2. Significant differences of the proportion in polecat diet were found for amphibians ($p<0.001$ for scats; $p<0.05$ for guts), carrion ($p<0.001$ in both samples) and mammals ($p< .01$ in scats; $p<0.05$ in guts). Other categories are of minor importance throughout the year, except possibly eggs.

Due to the dominance of anurans, the food niche is markedly narrower in summer than in winter. However, amphibians are also an important food in winter (48 % in december, 28 % in january, pooled data), when their activity is reduced or nil. Only in february was

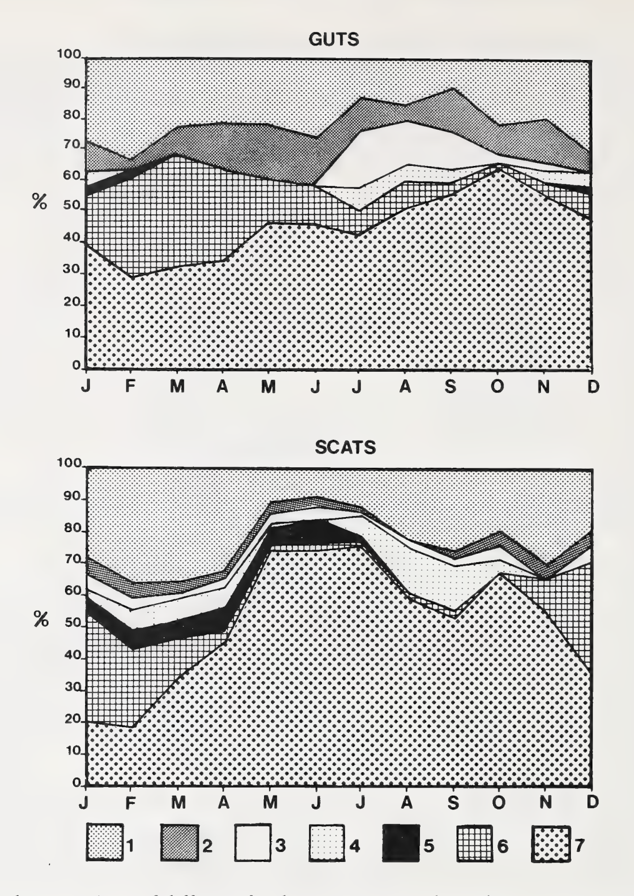


Fig. 1. Seasonal proportions of different food categories in polecat diet. Given are Gliding values over 3 months. Food categories given are mammals (1), birds/reptiles/fish (2), invertebrates (3), fruits (4), eggs (5), carrion/meat (6) and amphibians (7). Sample sizes (N) for single months are (guts/scats): J 12/26; F 5/34; M 9/34; A 8/30; M 14/21; J 8/47; J 3/8; A 16/20; S 17/15; O 15/8; N 18/1; D 15/11

this proportion slightly below 20 %. The reduced anuran contribution to diet is mainly compensated by an increase of the carrion/offal category. Monthly proportions of these two categories are strongly correlated ($r_s = -0.767$; $p < 0.001$).

Different treatment of scats (255 samples, 12 individuals) and guts (139 samples, 88 individuals) in tab. 2 shows that the above-mentioned seasonal differences in polecat diet are a general phenomenon in Switzerland; local specialities will be shown below.

Age- and sex-specific diets

The diet of juveniles is compared to that of adults (>1 year old) in the months of July to October, as juveniles occur per definitionem only during this period (tab. 2). There are significant differences for the occurrence of mammals ($p < 0.001$) and fruits ($p < 0.01$). The difference in the category of invertebrates is not significant ($p < 0.12$), presumably due to the small sample size. Reduced exploitation of mammals and compensation of this by feeding on fruits and invertebrates leads to a broader food niche in juveniles.

Scats were not used to investigate sexual differences in the diet, as there are no female

Table 2. **Dietary differences according to season, age and sex**

Period	Winter (XII.–IV.)		Summer (V.–XI.)		July–October		Whole year	
Sample	Guts All	Scats All	Guts All	Scats All	Guts/Scats pooled Juveniles	Adults	Guts Females	Guts Males
Mammals	24.5	31.5	19.8	15.2	6.5	32.2	25.0	24.2
Amphibians	34.4	34.1	53.8	66.7	55.6	54.4	44.3	44.0
Other vertebrates	10.4	4.1	12.1	2.7	8.6	8.9	14.3	9.7
Carrion/offal	25.0	18.5	5.5	2.5	5.1	2.2	11.4	19.0
Invertebrates	0.0	2.6	6.6	3.6	10.3	2.2	2.9	0.0
Eggs	1.6	3.9	0.0	4.2	0.0	0.0	2.1	0.0
Fruit	4.2	5.4	2.2	5.0	13.8	0.0	0.0	3.2
Sample size (N)	48	135	91	120	58	45	35	62
Niche breadth	3.94	3.90	2.85	2.11	2.83	2.45	3.41	3.35

The percentages of occurrence are given for seven main food categories. 28 scats of a female which lived exclusively on a rubbish-heap and foraged there on carrion and rats (all in October) are omitted in this table

droppings from winter and only those of three individuals in summer. This database would not allow individual variation to be separated from sex-specific variation. To obtain a sufficient sample-size, data from the whole year were pooled (Tab. 2). The data let not suspect sex-specific diets.

As polecats show a prominent sexual dimorphism, corresponding differences in prey size might be expected. An analysis of prey size was unfortunately not possible for anurans, the main dietary component: Intraspecific variation in the size of adult frogs and toads is considerable compared to mammals (Hintermann [1984] found in the Leimental area spawning *Rana temporaria*-females from 22 to 99 g), but the small anuran bone fragments could rarely be correlated to the size of the victim. Sex-specific proportions of different-sized prey species of mammals and invertebrates are given in tab. 3.

The table shows that male polecats do not exploit larger mammals than females. A statistical test (Kolmogorov-Smirnov-test for 2 samples) shows even the contrary ($D = 0.400$; $p < 0.025$). Pooling murids and microtids does not fundamentally change the image ($p < 0.05$). It must be stressed however, that the database is restricted, that the main prey (anurans) is not considered and that most hares are probably not killed, but found as carrion.

Table 3. **Occurence (%) of different-sized prey from the mammal/arthropod group in females and males**

Prey	Males	Females
Arthropoda	9.4	9.8
Soricidae	18.3	7.3
Apodemus, Mus	38.0	20.7
Microtus, Clethrionomys, Pitymys	25.8	25.6
Talpa, Glis, Arvicola	3.8	9.8
Rattus norvegicus	1.9	0.0
Erinaceus europaeus	0.9	0.0
Lepus capensis	1.9	31.8
Sample size (N)	53.25	20.5

Pooled data from all individuals exept one female, which lived on a rubbish-heap and foraged exclusively on rats and carrion. Size-classification of prey according to Brugge (1977) and Van den Brink (1975).

Regional variations in diet

Due to the mountain chains of the Alps and the Jura, ecological conditions in Switzerland range from arctic to submediterranean, altitude being the most important factor. I therefore investigated regional variations in polecat diet. The study areas "Leimental" and "La Brévine mountains" are described above. Guts were obtained from the whole country, which for the following analysis is divided into areas above and below 500 m of altitude.

The resulting four regions with different ecological conditions and human land use can be characterized as follows (Note that 1 and 4 are relatively homogenous; 2 and 3 very heterogenous areas):

1. 1000–1300 m: harsh winters (January mean −4 °C), conifer and mixed mountain forests, mountainous pastures, few, isolated farms (partly not used in winter).
2. 500–1000 m: cold winters (January mean −1 to −3 °C), mixed forests, dairy-farming, dispersed farms and habitats.
3. 250–500 m: mild winters (January mean +1 to −1 °C) decidous and mixed forests, mainly arable farming, farms and habitats concentrated in villages.
4. 300–450 m: similar to 3), but almost exclusively decidous forests and arable farming.

Polecat diets in these 4 regions are presented in fig. 2. Differences between regions are most pronounced during winter, when the food-niche in the mountains is narrower than in the lowlands. In the La Brévine mountains, anurans are the staple food throughout the year, with *Bufo bufo* dominating clearly. The relationship between altitude and the importance of anurans as polecat food was tested by a Mann-Whitney-U-test using all guts. This test confirms the impression from fig. 2 ($U = 2644$; $Z = 1.79$; $p < 0.05$). A multivariate approach, taking account of seasonal, sex- and age-related biases, would probably reveal a correlation of higher significance.

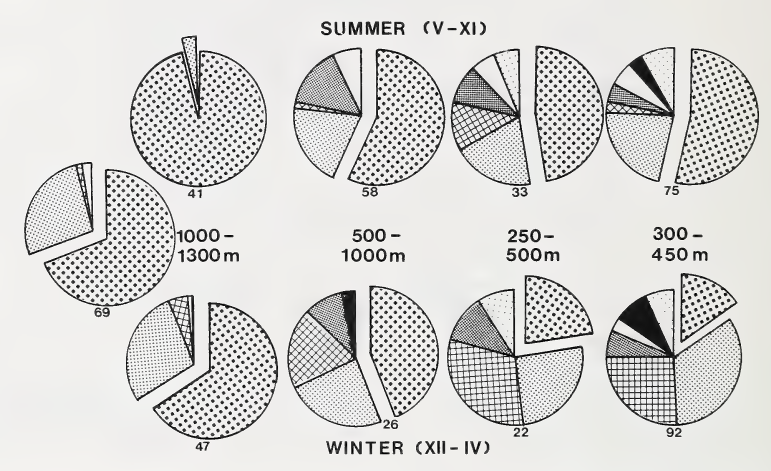


Fig. 2. Polecat diet in regions of different altitudes. Circle segments are proportional to frequency of occurrence. Categories identical to fig. 1. Amphibian segments are cut out. Data from scats (1000–1300 m; 300–450 m) and guts (500–1000 m; 250–500 m). At left 69 scats from autumn to winter which could not be dated exactly. Sample sizes (N) below circles

Discussion

Methodical weaknesses

Several authors have tried to correlate absolute quantities of food remains in scats and guts to quantities of food ingested (e.g. Erlinge 1981; Lockie 1961; Goszczynski 1976; Holisova and Obrtel 1982; Waechter 1975; Zielinsky and Spencer 1983). Correction factors for different items are thereby established on the basis of feeding trials. For four reasons, such attempts were not undertaken in the present study: i) The digestability of specific items can depend on the presence of other items. For example, polecats fed with pure meat excrete undigested meat cells; when meat is fed together with whole mice, no remains of the meat are found in the scats (pers. obs.). ii) Depending on the circumstances,

different parts of the same prey-type with different proportions of undigestable matter may be eaten (ERLINGE 1981): When many frogs are available, polecats may eat only the muscles of the hind legs, whereas in other circumstances the whole animal is eaten (WEBER 1987). iii) The same prey type may occur in different sizes (e.g. hares, rats, anurans), which can not necessarily be assessed using undigested remains. iv) In this study I was interested in the composition of typical polecat diets and not in the absolute amount of prey items eaten.

Thus, polecat diet was investigated by means of frequency analysis, which has often been used to evaluate mustelid diets (AMORES 1980; BRUGGE 1977; DANILOV and RUSAKOV 1969; ERLINGE and JENSEN 1981; KALPERS 1983; RASMUSSEN and MADSEN 1985; RAYMOND et al. 1984; ROSER and LAVERS 1976; RZEBIK-KOWALSKA 1972; TAPPER 1976 and others). Each scat and the contents of each stomach or intestine is considered as one independent sample of a polecat meal. Diet composition (not numbers of prey eaten) can be assessed accurately by this method, if only one prey-type is found per sample (ERLINGE 1981; DEBROT 1981; MOORS 1975; DAY 1968). In the present study this was mostly the case.

The occurrence of different prey types in the same sample presents the fundamental problem of frequency analysis. Some authors have tried to solve it by treating every identified prey item as the independent sample and by calculating frequencies of occurrence as the proportion of total items identified (e.g. DEBROT 1981; DANILOV and RUSAKOV 1969). A known disadvantage of this approach is the overestimation of small and rare dietary components (DEBROT 1981).

A lesser-known bias of the above mentioned approach is the overestimation of prey-types whose remains are defaecated over long periods. ROSER and LAVERS (1976) mentioned for ferrets *(Mustela putorius* f. furo) that anuran bones are defaecated more rapidly than mammal hairs. This is also supported by the observation during the present study that hair and feathers were more often found in small quantities than anuran bones (Tab. 4). Further support for this is given by the following observation: In 8 almost empty stomachs (< 1 ml) hairs were recorded but not amphibian bones, whereas in 77 stomachs with more than 1 ml of contents, anuran bones were present 34 times and hairs 20 times ($p < 0.001$). DEARBORN (1932) found feathers in the scats three days after feeding a sparrow to a mink *(Mustela vison)*. Meat remains would be defaecated by polecats within a few hours (GOETHE 1940). Thus, one mouse could leave detectable traces in dozens of scats, whereas the bones of a frog might be defaecated in one single dropping.

Table 4. **Occurrence of hairs, feathers and amphibian bones as bulk and as trace in guts and scats**

Estimatet percentage of sample volume	≥ 25 %	≤ 10 %
Hair/feather	149/16	47/8
Amphibian bones	255	13
$Chi^2 = 41$; $p << 0.001$		

Attempts to overcome these disadvantages by use of relative volume or weight of different items in a sample (RZEBIK-KOWALSKA 1972; HARGIS and MCCULLOUGH 1984) only make sense when all prey types have comparable proportions of undigestable matter. Amphibians and mammals do not fulfil this condition (BRUGGE 1977).

I have tried to minimize the biases mentioned above by disregarding stomach contents of less than 1 ml, and prey remains of less than an estimated 25 % of sample volume. Equal treatment of every identifiable item would have resulted in higher proportions of mammals and invertebrates. However, because only a minority of the samples contained more than one prey-type, such methodical differences are not sufficient to explain the differences of the results presented here to those of other studies.

The diet of polecats in Switzerland and elsewhere

Like other european *Mustela*-species (e.g. DEBROT 1981; ERLINGE 1981; MOORS 1975; KING 1980; CUTHBERT 1979) and in remarkable contrast to other mustelids of the region (WAECHTER 1975; TESTER 1986; MARCHESI 1985; BORN 1974) Swiss polecats are almost totally carnivorous.

The present study shows a dominance of anurans (mainly *Rana temporaria* and *Bufo bufo*) in the diet, which is most pronounced in summer and autumn. During this period more than half the prey are frogs and toads. In winter and spring, amphibians are partly replaced by carrion, and to a minor extent by mammals, but remain an important dietary component even during the coldest months. In the mountains, anurans are also the staple food in winter; specialization on amphibians is positivly correlated with altitude.

Invertebrates and fruits are taken mainly by juveniles, which show a correspondingly lower proportion of mammals in their diet than adults. Eggs have not often been found, but this may be due to a methodical bias. Personal observations of radio-tracked polecats (WEBER 1987) suggest a higher importance of this dietary component, especially in winter and spring.

These findings do not correspond very well to those of other authors in other countries, where far smaller percentages of anurans were found (Tab. 5). A proportion of more than 30 % was found only in the summer diet in northwest Russia. MERMOD et al. (1983) and WEBER (1986) out of 24 scats of Swiss polecats only found amphibian remains in one case.

Table 5. **Polecat diets from Germany (GOETHE 1939), Poland (RZEBIK-KOWALSKA 1972), Northwest Russia (DANILOV and RUSAKOV 1968). Czechoslovakai (KRATOCHVIL 1952) and the Netherlands (BRUGGE 1977)**

	Winter			Summer		Whole year	
	Russia	Poland	Germany	Russia	Poland	Czechosl.	Netherlands
Small mammals	51	17	37	52	14	47	32
Lagomorphs	1	2	4	0	7	10	29
Amphibians	19	11	18	32	19	18	20
Other vertebrates	9	20	14	11	25	14	20
Carrion/meat	18	27	2	2	10	0	0
Invertebrates	0	1	10	0	10	12	0
Eggs	0	17	17	0	14	0	0
Fruit	3	5	0	2	2	0	0
Sample size (N)	65	220*	57	26	44*	35	41

* 62 empty stomachs included. – All data from gut contents, partly recalculated to give % frequencies of occurrence.

Only LABHARDT (1980) observed in the Leimental area a female which brought 61 % anurans to her young (61 prey identified). GOETHE (1939) mentions that amphibians may dominate polecat diet in summer.

I see three factors that may explain the discrepancy of my results with most published data on polecat diet: i) methodical biases, ii) sampling biases, iii) local dietary specialization of polecats.

DANILOV and RUSAKOV (1968), RZEBIK-KOWALSKA (1972), BRUGGE (1977) and KRATOCHVIL (1952) have certainly overestimated the importance of mammals and birds in relation to amphibians, using also almost empty stomachs and considering all identified remains as single samples, regardless of their relative contributions to the sample volume (see discussion above). These biases have already been recognized and mentioned by

Brugge. However, this explanation is not sufficient to explain all discrepancies; a calculation of the diet composition of Swiss polecats using the methods of the papers cited above, still shows anurans as the staple food.

Radio-tracked polecats foraged exclusively in forests and in and around human buildings. In forests, mainly anurans were taken; in settlements none (Weber 1987). The gut collections of other authors were possibly habitat-biased. The high proportions of eggs found by Rzebik-Kowalska may be an indication of such a bias. As the studies mentioned in tab. 5 are based on gut analysis, presumably from shot or trapped polecats, a habitat bias in polecat hunting could explain the small numbers of amphibians.

It is not clear, why Swiss polecats should specialize on other prey than those elsewhere. Only the polecats in the Netherlands intensively use a ressource, which does not exist in Switzerland (rabbits). After declining during the last 50 years (Baumgartner 1986), amphibians do not seem to be more abundant in Switzerland at present than in Central and Eastern Europe dozens of years ago. However, the data from Switzerland show in winter low proportions of anurans in the lowlands. In these regions, foraging during the cold season is concentrated in and around barns and farmhouses. High anuran proportions in the mountains can be explained by poor food resources around farmhouses and, as a consequence, continued foraging in forests also during winter (Weber 1987). Therefore, at least in winter, a lower significance of frogs and toads as polecat food can also in Switzerland be expected outside mountainous areas, as has been shown in fig. 2.

Sexual dimorphism and diet

Sexual dimorphism of body size is a characteristic feature of mustelids, males always being larger than females. Two different theories were proposed to explain this dimorphism (for an extensive discussion hereon see Moors 1980): The first theory (e.g. Brown and Lasiewski 1972) claims that sexual dimorphism is a strategy for avoiding intraspecific competition, allowing each sex to exploit different food-resourcers. A more recent theory explains sexual dimorphism by different sex-specific pressures (females being selected for small size because of lower maintenance costs, and males being selected for successful intrasexual competition for mates; Erlinge 1979; Moors 1980; Raymond et al. 1983).

Discussion on the significance of the two competing theories concentrated until now on theoretical arguments and data from *Mustela erminea* and *M. nivalis*. Unfortunately, as far as is known, these species show not only the polygynous mating system with no male assistance in cub-rearing (argument for the second hypothesis), but also sex-specific diets with males killing larger prey than females (argument for the first hypothesis). So far, it is not clear whether food specialization is the cause or simply one consequence of sexual dimorphism.

The data presented here are, as those of Brugge (1977), arguments against the Brown and Lasiewski theory. The smaller females do not prey on smaller animals than males. It is highly probable that the situation is even inverse ($p < 0.025$). If polecats showed a similar mating system to that of stoats, *Mustela putorius* would be a stronger argument for the theory of Erlinge and Moors than *Mustela erminea*. Such a mating system may be indicated by the observation of a dramatic fat loss of male polecats during the mating season, whereas females loose their reserves during cub-rearing (Weber 1987).

The food niche of polecats and other mustelids

Polecats occur in Switzerland together with closely related (stoat, *Mustela erminea*) and similar-sized (pine marten, *Martes martes*, stone marten, *M. foina*) mustelids. According to "Gause's hypothesis" (Krebs 1978) long-term coexistence of different species is only possible where their niches differ significantly. Rosenzweig (1966) explained the coexist-

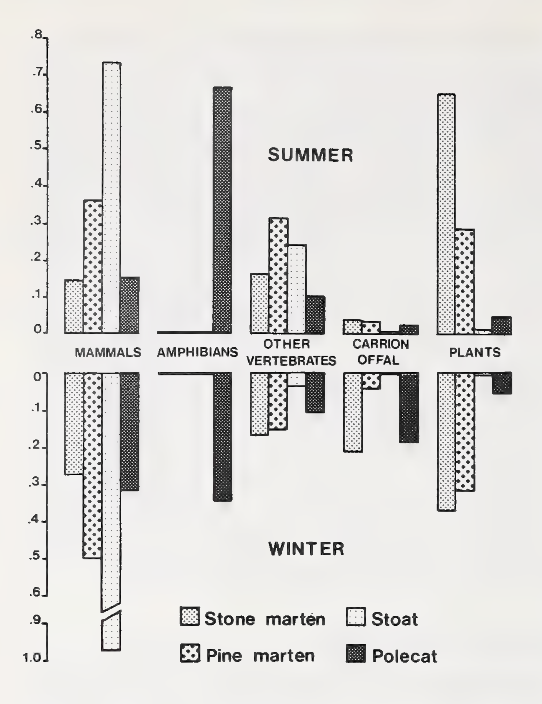


Fig. 3. Diet of 4 mustelids from Switzerland. Proportions of each of the five food categories are given for every species in summer and winter (sources see tab. 6)

ence of three species of weasel in North America with size-specific food specialization. Local dietary differences have been described for European *Mustela nivalis* and *M. erminea*. Powell and Zielinski (1983) have however shown theoretically that even partly overlapping food-niches make the long-term coexistence of two or more *Mustela*-species impossible, if no other fundamental biological differences occur. Newer theories explain the coexistence of *M. erminea* and *M. nivalis* with other interspecific differences than Rosenzweig (Simms 1979; King and Moors 1979). As rabbits occur only locally in Switzerland, there is no larger prey-class available for polecats than for stoats. Stoats are morphologically better adapted to vole-hunting than polecats. On the other hand, all resources used by polecats are also accessable to stone martens and pine martens.

Fig. 3 shows that polecats probably escape competition for food by

Table 6. **Overlap of food-niches of polecat (present study, gut contents), stone marten (Waechter 1975; Tester 1985), pine marten (Marchesi 1986) and stoat (Debrot 1981) in Switzerland**

Summer data of stone marten are means from Waechter and Tester, winter data are from Tester. Niche overlap is calculated as $O_{xy} = 1–0.5\ \Sigma\ |p_{ix} - p_{iy}|$ (Mühlenberg 1976), based on food-categories mammals, birds, reptiles, amphibians, fish, invertebrates, carrion/offal, fruit/plant

	Winter/Spring			Summer/Autumn		
	M. putorius	*M. foina*	*M. martes*	*M. putorius*	*M. foina*	*M. martes*
Martes foina	0.535	–	–	0.339	–	–
Martes martes	0.374	0.760	–	0.390	0.623	–
Mustela erminea	0.265	0.286	0.526	0.358	0.318	0.533

Table 7. **Records interpreted as amphibian gut contents**

Item	N records	Item	N records
Pulmonata	4	Formicidae	19
Diplopoda	1	Div. Hymenoptera	4
Tettigonioidea	2	Lepidoptera	2
Grylloidea	1	Nematocera	3
Dermaptera	7	Brachycera	4
Heteroptera	4		
Coleoptera	29	Unid. Arthropoda	15

specialized preying on frogs and toads, which are not systematically exploited by other mammals (Note that all data in fig. 3 originate from the polecat-study areas Leimental [WAECHTER 1975; TESTER 1986] and La Brévine mountains [DEBROT 1981; MARCHESI 1985] or nearby sites). The realized food niches of stoats, stone martens and pine martens show larger overlaps between themselves than with that of the polecat (Tab. 6). The only exception to this is the apparent niche overlap in winter between stone marten and polecat. This is due to an undifferentiated analysis of the mammalian component of their respective diets. A more detailed comparison shows that the bulk of mammals eaten by stone martens are voles (70 %), whereas voles only account for about 30 % of the mammals in the polecat diet.

One can conclude that Swiss polecats considerably reduce potential food competition with other mammals by specialising on frogs and toads. On the other hand one has to note that the consequence of this freedom from competition is the highest trophic position of all terrestrial mammals in the region.

Acknowledgements

I thank U. RAHM for encouraging me to undertake this study; A. WANDELER, H. LETHIER, for making available polecat stomachs; F. LABHARDT, for precious advice in laboratory techniques; J.-M. WEBER and P. MARCHESI, for capturing polecats in the La Brévine region and for advice in hair identification techniques. I am most grateful to everyone who sent polecat carcasses and regret that there is not sufficient space to name them all. My English was corrected by J. TAYLOR. This research was supported by the "Basler Stiftung für die biologische Forschung" and the "Brunette Stiftung für Naturschutz". The paper was written with the support of the "Geiby-Jubiläums-Stiftung".

Zusammenfassung

Zur Nahrung des Iltisses (Mustela putorius L.) in der Schweiz

Die Nahrung schweizerischer Iltisse wurde durch die Analyse von Magen-Darm-Inhalten von 120 zwischen 1982 und 1987 gestorbenen Individuen sowie durch die Analyse unverdauter Reste in 354 Losungen von mindestens 12 Individuen untersucht. Iltiskadaver erhielt ich aus der ganzen Schweiz und angrenzenden Gebieten Frankreichs. Fast alle Losungen stammen von 12 mit Radiosendern markierten Tieren aus dem Leimental bei Basel (300–450 m) und dem Neuenburger Jura (1000–1300 m). Reste von Iltismahlzeiten bilden eine weitere Informationsquelle. Quantitative Aussagen erfolgen auf der Basis gewichteter Frequenzen, wobei Reste, die deutlich weniger als 25 % der einzelnen Stichprobe (Losung, Mageninhalt, Darminhalt) ausmachten, nicht berücksichtigt wurden.

Schweizerische Iltisse ernähren sich fast ausschließlich carnivor. In einem geringen Ausmaß werden, hauptsächlich von Jungtieren, auch Früchte aufgenommen. Als Nahrungsbestandteile konnten 43 Tierarten, 8 Pflanzenarten sowie Fleischabfall und Haustierfutter nachgewiesen werden. Die dominierende Nahrungskomponente bilden Anuren. Weitere Nahrungskomponenten von Bedeutung sind Kleinsäuger (hauptsächlich Muridae, aber auch Microtidae und Soricidae), Aas und Fleischabfall aller Art und Eier von Hausgeflügel.

Der Anurenanteil der Nahrung ist im Winter geringer als im Sommer und in Berggebieten höher als im Tiefland. In Berggebieten sind Anuren auch im Winter die wichtigste Nahrungskomponente. Jungtiere fressen häufiger Invertebraten und Früchte, dafür seltener Kleinsäuger als adulte Iltisse. Eine unterschiedliche Bedeutung der Nahrungskategorien Amphibien, Säuger, andere Vertebraten, Invertebraten, Aas/Fleischabfall und Früchte in der Nahrung der beiden Geschlechter zeigte sich nicht. Weibchen bevorzugten innerhalb der Gruppe Säugetiere/Arthropoden größere Beutetiere als männliche Iltisse.

Die angewandten Methoden und die Ergebnisse werden unter verschiedenen Gesichtspunkten diskutiert und mit Literaturangaben verglichen. Die Nahrung schweizerischer Iltisse unterscheidet sich durch den hohen Anurenanteil stark von Befunden aus anderen Gebieten. Die Nahrungsnische schweizerischer Iltisse überlappt nur wenig mit denjenigen anderen Musteliden, welche untereinander dagegen teilweise starke Nischenüberlappung zeigen. Iltisse besetzen die höchste trophische Position aller terrestrischen Carnivoren des Gebietes. Die Ernährung des Iltisses bildet ein wichtiges Zusatzargument in der Debatte um die Ursachen des Geschlechtsdimorphismus in der Gattung *Mustela*.

References

Amores, F. (1980): Feeding habitats of the stone martens, *Martes foina* (Erxleben, 1777) in south western Spain. Säugetierk. Mitt. **28,** 316–322.
Ashby, K. R.; Elliot, K. (1983): The diet of the badger (*Meles meles* L.) in Castle Eden Dene, Country Durham. Acta Zool. Fennica **174,** 205–207.
Baumgartner, H. (1986): Amphibien der Schweiz. Panda **19,** 1–32.
Born, E. (1974): Zur Biologie des Dachses in der Region Basel. Unpubl. Diplomarbeit, Universität Basel.
Brohmer, P. (1971): Fauna von Deutschland (12. Auflage). Heidelberg: Quelle und Meyer.
Brown, J. H.; Lasiewski, R. C. (1972): Metabolism of weasels: The cost of being long and thin. Ecology **53,** 939–943.
Brugge, T. (1977): Prey selection of weasel, stoat and polecat in relation to sex and size. Lutra **19,** 39–49.
Cuthbert, J. H. (1979): Food studies of feral mink *(Mustela vison)* in Scotland. Fish Manage **10,** 17–25.
Danilov, P. I.; Rusakov, O. S. (1969): (Special aspects of the ecology of the polecat *[Mustela putorius]* in the north-west regions of the European U.S.S.R.). Zool. Zh. **48,** 1383–1394.
Day, M. G. (1968): Food habits of British stoats *(Mustela erminea)* and weasels *(Mustela nivalis).* J. Zool. **125,** 485–497.
Dearborn, N. (1932): Food habits of some predatory fur bearing animals in Michigan. Univ. Michigan School of Forestry and Conservation Bull. **1,** 1–25.
Debrot, S. (1981): Trophic relations between the stoat *(Mustela erminea)* and its prey, mainly the water vole (*Arvicola terrestris* sherman). In: Proc. Worldwide Furbearer Conf. Ede. by J. A. Chapman Frostburg, USA. 1259–1289.
Debrot, S.; Fivaz, G.; Mermod, C.; Weber, J.-M. (1982): Atlas des poils de mammifères d'Europe. Inst. Zool. Université Neuchâtel.
Eiberle, K. (1969): Vom Iltis *(Mustela putorius)* in der Schweiz. Schweiz. Z. Forstwesen **120,** 99–107.
Erlinge, S. (1979): Adaptive significance of sexual dimorphism in weasels. Oikos **33,** 233–245.
— (1981): Food preference, optimal diet and reproductive output in stoats *Mustela erminea* in Sweden. Oikos **36,** 303–315.
Erlinge, S.; Jensen, B. (1981): The diet of otters *Lutra lutra* in Denmark. Natura Jutlandica **19,** 161–165.
Goethe, F. (1939): Untersuchungen über die Winternahrung des Illtis nebst einigen weiteren biologischen Feststellungen. Wild und Hund **43,** 720–722.
— (1940): Beiträge zur Biologie des Iltis. Z. Säugetierkunde **15,** 180–221.
Goszczynski, J. (1976): Composition of the food of Martens. Acta Theriol. **21,** 527–534.
Hargis, C. D.; McCullough, D. R. (1984): Winter diet and habitat selection of marten in Yosemite Nationalpark. J. Wildl. Manage. **48,** 140–146.
Hintermann, U. (1984): Populationsdynamische Untersuchungen am Grasfrosch *Rana temporaria* Linnaeus, 1758 (Salientia, Ranidae). Salamandra **20,** 143–166.
Holisova, V.; Obrtel, R. (1982): Scat analytical data on the diet of urban stone martens, *Martes foina* (Mustelidae, Mammalia). Folia Zool. **31,** 21–30.
Kalpers, J. (1983): Contribution à l'étude eco-ethologique de la fouine *(Martes foina)*: Stratégies d'utilisation du domaine vital et des ressources aliméntaires (1): Introduction générale et analyse du régime alimentaire. Cahiers d'Ecologie Appliquée **3,** 145–163.
King, C. M. (1980): The weasel *Mustela nivalis* and its prey in an English woodland. J. Anim. Ecol. **49,** 127–159.
King, C. M.; Moors, P. J. (1979): On coexistence, foraging strategy and the biogeography of weasels and stoats in Britain. Oecologia (Berl.) **39,** 129–150.
Kratochvil, J. (1952): (La nourriture et les races du *Putorius putorius* L.). Acta Univ. Agriculturae Silviculturae Brno **1,** 43–60.
Krebs, C. J. (1978): Ecology, 2nd ed. New York: Harper and Row.
Labhardt, F. (1980): Zur Fütterungstätigkeit und über einige Verhaltensweisen einer freilebenden Iltisfähe, *Mustela putorius* Linne, 1758. Säugetierk. Mitt. **28,** 247–251.
Lockie, J. D. (1961): The food of the pine marten *Martes martes* in West Ross-shire, Scotland. Proc. Zool. Soc. London **136,** 187–195.
Marchesi, P. (1985): Ecologie de la martre (*Martes martes* L.) en forêt montagnarde du Jura suisse: Résultats préliminaires. In: Trans. 17. Congr. Int. Union Game Biol. 1985. Ed. by. S. A. Crombrugghe. Bruxelles. 303–310.
Mermod, C.; Debrot, S.; Marchesi, P.; Weber, J.-M. (1983): Le putois (*Mustela putorius* L.) en Suisse romande. Rev. Suisse Zool. **90,** 847–856.
Moors, P. J. (1975): The food of weasels *(Mustela nivalis)* on farmland in northeast Scotland. J. Zool. **177,** 455–462.

— (1980): Sexual dimorphism in the body size of mustelids (Carnivora): The roles of food habits and breeding systems. Oikos **34**, 147–158.

MÜHLENBERG, M. (1976): Freilandökologie. Heidelberg: Quelle und Meyer.

MÜRI, H. (1982): Baum- und Steinmarder. Wildbiologie für die Praxis **1**, 11 pp.

POWELL, R. A.; ZIELINSKI, W. J. (1983): Competition and coexistence on mustelid communities. Acta Zool. Fenn. **174**, 223–227.

RASMUSSEN, A. M.; MADSEN, A. B. (1985): The diet of the Stone Marten *Martes foina* in Denmark. Natura Jutlandica **21**, 141–144.

RAYMOND, M.; BERGERON, J.-M.; PLANTE, Y. (1984): Dimorphisme sexuel et régime alimentaire de l'hermine dans un agrosystème du Quebec. Can. J. Zool. **62**, 594–600.

ROSENZWEIG, M. L. (1966): Community structure in sympatric Carnivora. J. Mammalogy **47**, 602–612.

ROSER, R. J.; LAVERS, R. B. (1976): Food habits of the ferret (*Mustela putorius* L.) at Pukepuke Lagoon, New Zealand. New Zeal. J. Zool. **3**, 269–276.

RZEBIK-KOWALSKA, B. (1972): (Studies on the diet of te carnivores in Poland). Acta Zool. Caracoviensia **17**, 415–506.

SCHAEFER, H. (1932): Die Artbestimmung der deutschen Anuren nach dem Selet. Z. Anat. Entw.-gesch. **97**, 767–779.

SIEGEL, S. (1956): Nonparametric statistics for the behavioral sciences. Tokyo: McGraw-Hill.

SIMMS, D. A. (1979): North American weasels: resource utilization and distribution. Can. J. Zool. **57**, 504–520.

STRESEMANN, E. (1974): Exkursionsfauna. Wirbeltiere (6. Auflage). Berlin: Volk und Wissen.

TAPPER, S. C. (1976): The diet of weasels, *Mustela nivalis* and stoats, *Mustela erminea* during early summer, in relation to predation on gamebirds. J. Zool. **179**, 219–223.

TESTER, U. (1986): Vergleichende Nahrungsuntersuchung beim Steinmarder *Martes foina* (ERXLEBEN, 1777) in großstädtischem und ländlichem Habitat. Säugetierkundl. Mitt. **33**, 37–52.

VAN DEN BRINK, F. H. (1975): Die Säugetiere Europas (3. Aufl.). Hamburg: Verlag P. Parey.

WAECHTER, A. (1975): Ecologie de la fouine en Alsace. Terre et Vie **29**, 399–457.

WEBER, D. (1987): Zur Biologie des Iltisses (*Mustela putorius* L.) und den Ursachen seines Rückganges in der Schweiz. Unpubl. Diss. Univ. Basel. 194 pp.

— (1986): Aspects quantitatifs du cycle de Skrjabingylus nasicola (Leuckart, 1942) nematode parasite des sinus frontaux des mustelides. Diss. Univ. Neuchatrel.

ZIELINSKI, W. J.; SPENCER, W. D. (1983): Relationship between food habits and activity patterns of pine martens. J. Mammalogy **64**, 387–396.

Author's address: Dr. DARIUS WEBER, Ökologische Beratung und Systemanalysen, Talackerstraße 23, CH-4153 Reinach, Schweiz

Z. Säugetierkunde 54 (1989) 172–190

ISSN 0044-3468

The external forces and internal stresses in the feet of dressage and jumping horses

By H. Preuschoft

Funktionelle Morphologie, Anatomisches Institut, Ruhr-Universität Bochum

Receipt of Ms. 13. 10. 1987

Abstract

From motion pictures taken at 200 f/s over standardized distances we measured the movements performed by the joints of horses in dressage gaits and in jumping under saddle in two dimensions. Velocities and accelerations of the whole body and its segments were calculated. With segment masses taken from the literature, the "external" forces acting on the segments were computed. The results obtained this way are in principal agreement with the accelerations and reaction forces measured during the same movements. The forces exchanged between the horse's body and the ground are mostly 2 times, sometimes up to 4 times body weight, but distributed over several extremities and fairly long time intervals. The reaction forces transmitted by a single limb in take-offs for, and in landings after a jump, but also in the dressage gaits called by Germans "starker Trab" and "starker Galopp" may lead to stresses beyond the presumed breaking strength. This in particular, if the positions of the distal extremity segments are suboptimal.

Introduction

In mammals, the shape of the body is dominated by the locomotor apparatus. Therefore we have to look after the locomotor behavior, if we wish to understand the reasons for the development of a certain body shape in an animal. This idea is by no means new, but a truly satisfying basis for the recognition of the causal relationship between form and mechanical function has been established as late as 1935–1964 by the orthopedist F. Pauwels (see also 1965). Kummer (1959) has applied Pauwels' principles to the body shape of mammals, and Preuschoft (1969, 1970a, b, 1973, 1979, 1988; Preuschoft et al. 1986) has continued this line by explaining details of primate skeletal morphology in terms of mechanics.

These considerations, however, are restricted to "long term stresses", that is, they are focussed on static situations and do not imply the time factor – neither as resistence against being moved (mass inertia), nor as the variation of external forces during time, which lead to "short term stresses".

Now we can raise new questions:

- Which stresses do occur in parts of the animal's body in more rapid movements?
- Is the shape of the element suited to sustain these stresses?

The parameters essential to answer these questions are the resultant forces acting in the joints, and the stresses in the bones. Both can not be measured directly without negative influence on the moving system. In addition, direct measurements of the strains inside the moving body are difficult to obtain, and the procedure to get them is noxious to the animal. So we used a combination of indirect approaches to obtain these values.

Our mechanical analyses are based on d'Alemberts' principle, according to which movements can be analysed as sequences of phases in which equilibrium exists between the activity of muscles on one side and the mass inertia of body segments on the other. Inertia tends to keep mass elements in their state of movement, and exerts a force which resists any change of direction or velocity. The forces caused by inertia depend on the masses of the involved body segments times their accelerations.

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5403-0172 $ 02.50/0

We used the following data: masses of segments, and either the displacements in space of body segments over time (in the form of film recordings), or the forces which act on the animal's body (force plate recordings), or accelerations of segments (data from accelerometers).

To secure the relevance of the analyses, we also need information about the biological importance of the analysed movement. The simplest and most reliable criterion seems to be the statistical frequency of its occurrence. There is considerable uniformity of opinion that frequent, though low stresses exert a decisive influence on the shapes of bones and tendons, while greater stresses, which occur less frequently, may have a higher threshold. Very rare stress patterns, which are evoked in long intervals may fall outside the "average biomechanic situation" to which the body shape is adapted (see for instance AMTMANN 1979; OXNARD 1979; PREUSCHOFT 1979, 1985). It seems safe to start from the assumption that the locomotor apparatus of an animal is adapted to sustain even the highest among the "usually", or "normally" occurring stresses. Therefore we first have to determine the "normal" loading pattern of the skeletal and tendinous elements, evoked in movements, which are executed often and without inflicting damage to the animal. The highest among the (statistically defined) "normal" stresses should encompass what the animal's body can sustain. On the same basis, we can define those situations, in which the stresses reach critical values.

Motion analyses in some cases also allowed us to approach the question how the proportions of and the mass distribution in the body fit to the pattern of locomotion (CARTMILL 1974; ALEXANDER et al. 1979; MCMAHON 1984; JUNGERS 1984, 1985; PREUSCHOFT and DEMES 1984, 1985; PETERS and PREUSCHOFT 1984; DEMES and GÜNTHER 1988; DEMES et al. 1988).

For studies of the type described above, the outstanding subjects are, aside from humans, horses. This because of various reasons:
- They show (and seem to be designed for) a limited variation of movements;
- these are largely restricted to only two dimensions;
- they can be reproduced reliably, in particular if performed under a rider;
- the animals are big and strong enough to carry the measuring equipment without disturbance of their movements.

In the focus of our interest have been the most specialized body segments: the "foot" in an anatomical sense, that is carpus, tarsus, metapodials and phalanges. These parts are under immediate influence of external forces, and in addition the experience of horsemen tells us that these parts are loci of predilection for failure.

Material and methods

The investigations were made with successful and high class dressage (1), event (2) and jumping horses (6) from the stable of the Deutsches Olympia-Kommittee für Reiterei (DOKR), Deutsche Reiterliche Vereinigung (FN) in Warendorf; one dressage horse owned by O. RHODE, Oer-Erkenschwick. Preliminary experiments to optimize the techniques have been made on the 2 German saddle horses of H. DALLMER, Arnsberg, and most of them on my own lightweight hunter of Irish origin. All these horses are trained according to the German dressage method. Therefore I also use the terminology usual in this country for the investigated gaits (see, for instance, PODHAJSKY 1968).

1. A Philips three dimensional accelerometer (PR 9369/50) with an own frequency of 3000 Hz was fixed to the saddle, close to the presumed center of gravity of the system: horse + rider (fig. 1). Its signals were telemetered through a transmitter in a saddle bag. The recieved signals were controlled on an oscilloscope and stored on a tape recorder. For evaluation, the recordings were plotted on a 6 channel printer at a paper velocity of 100 mm/s.

2. Deformations of the hoof during movement were measured with strain gages attached to the external surface of the hoof (fig. 2), and by strain gages on a spring steel band connecting medial and lateral margins of the hoof (fig. 3). The signals were transmitted through wires to the saddle bags, and recorded as before.

Unfortunately, only a small portion of these measurements could be taken synchronously with other recordings.

3. Measurements of the vertical and sagittal ground reactions by means of a home-made, triangular force plate, fit into a 7 m × 0,6 m wooden platform allowed at least in some cases a control of the ground-foot-forces obtained by calculations. The force plate recordings are very similar to those obtained from hoof deformations. There were, however, no means to calibrate the deformations of the hooves against the transmitted load.

4. High speed films were taken by the Institut für den Wissenschaftlichen Film, Göttingen at 200 f/s. The joints of the horses were marked with water-soluble colours. At constant distance of 60 m from the camera, a course of 32 m (dressage) and 48 m (jumps) length was staked out by red and white poles in 2,0 m (dressage) and 3,0 m (jumps) distance (for more details, see Preuschoft et al. 1987). The bases of these poles were connected by a red and white ribbon to indicate the horizontal. The riders were instructed to go as close to the poles as possible. The distances of the tracks from the rails turned out to vary by not more than 0.3 m.

Kinematic parameters, such as speed, stride length, frequency, duration of swing and stance phase, width and duration of suspension, angle of limb axis, path of accelerometer and other points were investigated statistically (for details see Preuschoft et al. 1987). Cycles and jumps which represent average values of these parameters were selected for digitizing.

5. Horse plus rider form a kinematic chain of 26 rigid links. The vertical and horizontal displacements of the joints were plotted against time, thus yielding the translatory and rotatory velocities of the segments.

By differentiation of the velocities we arrive at their accelerations. Resistence to being moved is given by the forces of inertia (= acceleration times mass). These forces have been calculated for each time interval. Segment masses are taken from Plagenhoef (1979).

The forces calculated for the segments in vertical, sagittal and rotatory direction are summed up. The only points through which forces can be transmitted from the ground to the animal's body are the hooves.

As long as no rotation takes place, rotating moments about the center of gravity must be zero. Therefore in phases with two hooves on the ground an exact distribution of the vertical (but not of the horizontal) components on the limbs is possible. In phases with 3 or 4 limbs in ground contact, we distributed the components so on the footing limbs, that the resultant reaction force is more or less parallel to the metapodials, because this minimizes the bending moments. Under the assumption that the forces are concentrated on the middle of the hoof, the rotating moments of the resultant external force at the interphalangeal and metapodial joints can be calculated (fig. 4). This was done only for those phases in which the external forces assume their highest values.

6. Maintenance of equilibrium at the joints requires tensile forces in the tendons and ligaments of the foot. From the external force acting against the hoof and the tensile forces in the tendons result compressive forces and bending moments in the phalanges and metapodials (as shown in fig. 2). Cross sections of the joints and metapodia, as well as lever lengths are as in Preuschoft and Fritz (1979).

Results

Some parameters, such as stride lengths and frequencies show surprisingly little variation within the cycles of one run, within the runs of one horse, and from one horse to the other (table 1). This is, however, not more than a confirmation of common knowledge, on which the internationally used principles of judging horse shows are based.

Other gait parameters, such as accelerations, or heights reached by the distal limb segments during swing phase, or strain of the hooves, or the measured intervals of force exchange vary considerably (table 2) – in particular if taken from a horse running on a rough substrate.

The deformations of the external surface of the hooves show a slow increase and a steep decrease (fig. 2). This result is not identical with the recordings obtained by Bayer (1973), and also deviates from our measurements of the width of the hoof during ground contact (fig. 3). According to measurements taken on isolated hooves under a hydraulic press, the deformations are not linearly correlated with load, and show pronounced hysteresis. Since we were not able to calibrate the deformations of the external wall in the living horse, we abandoned this method.

Hoof width increases in the stance phase by 0.05 to 1.9 mm, averages are given in table 2. It reaches a plateau in the walk, but shows a clearcut parabolic peak in all faster gaits (fig. 3). The deformation of the hoof is the more pronounced the faster the horse moves, regardless

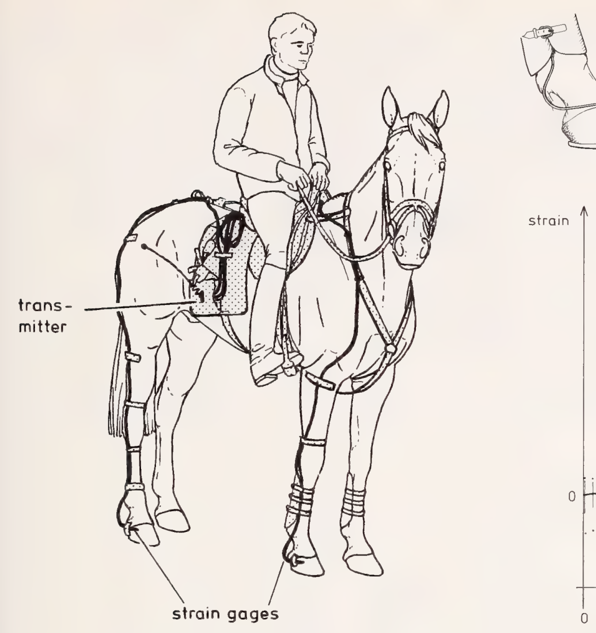


Fig. 1. Horse equipped with strain gages at right front and right hind hooves, accelerometer at saddle, teletransmitter in saddle poaches. The markings at the joints are on the left side and therefore not visible

Fig. 2. Recordings of a strain gage during trot ("starker Trab"). The vertical bars crossing the graph are ± standard deviations out of 9 cycles, the dots deliminate the range of variation. The insert shows how the strain gages were attached to the hoof

Table 1. **Examples of kinematic parameters showing limited variation**

	Trot				Galop			
	$\bar{x}$	sd	v.c.	n	$\bar{x}$	sd	vc %	n
Cycle duration [s] „Arbeitstrab" „Arbeitsgalopp" 1 horse, 3 runs for each gait	0.75	0,03	4.12 %	126	0.64	0.03	4.69 %	180
Frequency [cycles/min] „Mitteltrab" „Mittelgalopp" 3 horses	83.90	1.50	1.78 %	28	104.80	1.70	1.62 %	60
Stride length [m] „Mitteltrab" „Mittelgalopp" 3 horses	3.48	0.15	4.19 %	76	300.50	12.02	4.00 %	120
Stride length [m] „Mitteltrab" „Mittelgalopp" 3 horses	3.43	0.15	4.23 %	28	3.19	0.12	3.60 %	60

Table 2. **Examples of kinematic parameters showing extensive variation 3 horses, 1 run each**

	Trot („Mitteltrab")				Galop („Mittelgalopp")			
	$\bar{x}$	sd	v.c.	n	$\bar{x}$	sd	vc %	n
Vertical acceleration [m/s^2]	17.43	3.73	21.40 %	28	15.43	2.85	18.47 %	60
Horizontal acceleration [m/s^2]	10.56	3.57	33.80 %	28	10.85	3.16	29.12 %	60
Maximal height front + hind hooves [cm]	24.84	2.25	9.06 %	76	25.02	2.08	8.33 %	120
Medio-lateral strain of hoof [mm]	0.43	0.13	30.40 %	23	0.38	0.15	40.06 %	41
Loading time [s]	0.34	0.04	10.75 %	69	0.28	0.02	8.63 %	82

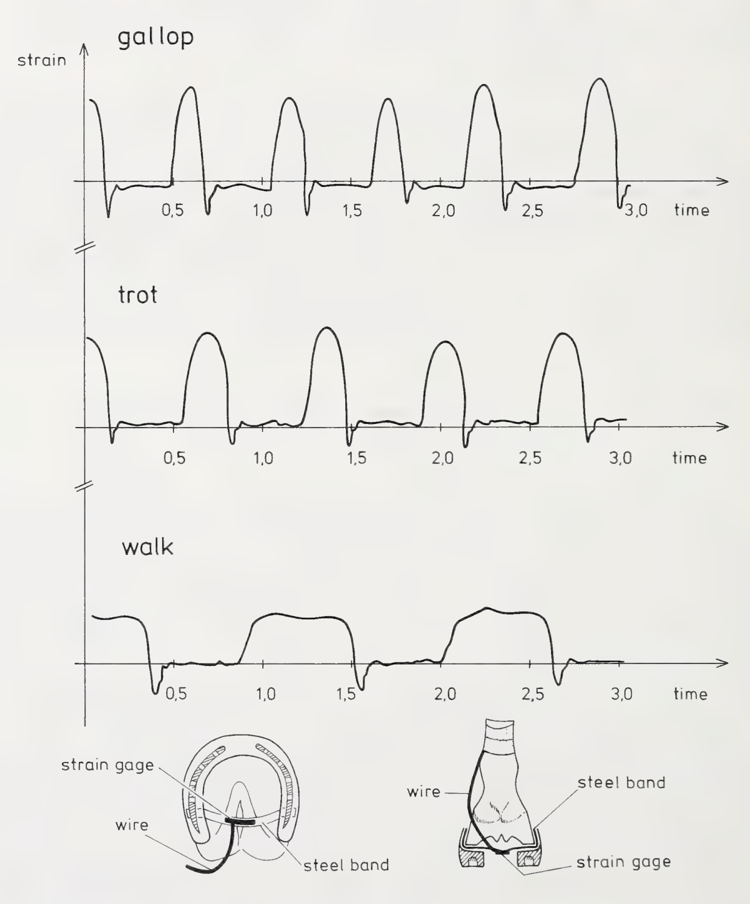


Fig. 3. Width changes over time of the front hoof in transverse direction, measured by the device shown at the bottom. It is protected by "Dallmer Hufschuh". Examples of various gaits: walk, trot, gallop on a hard substrate (concrete), same horse in all cases

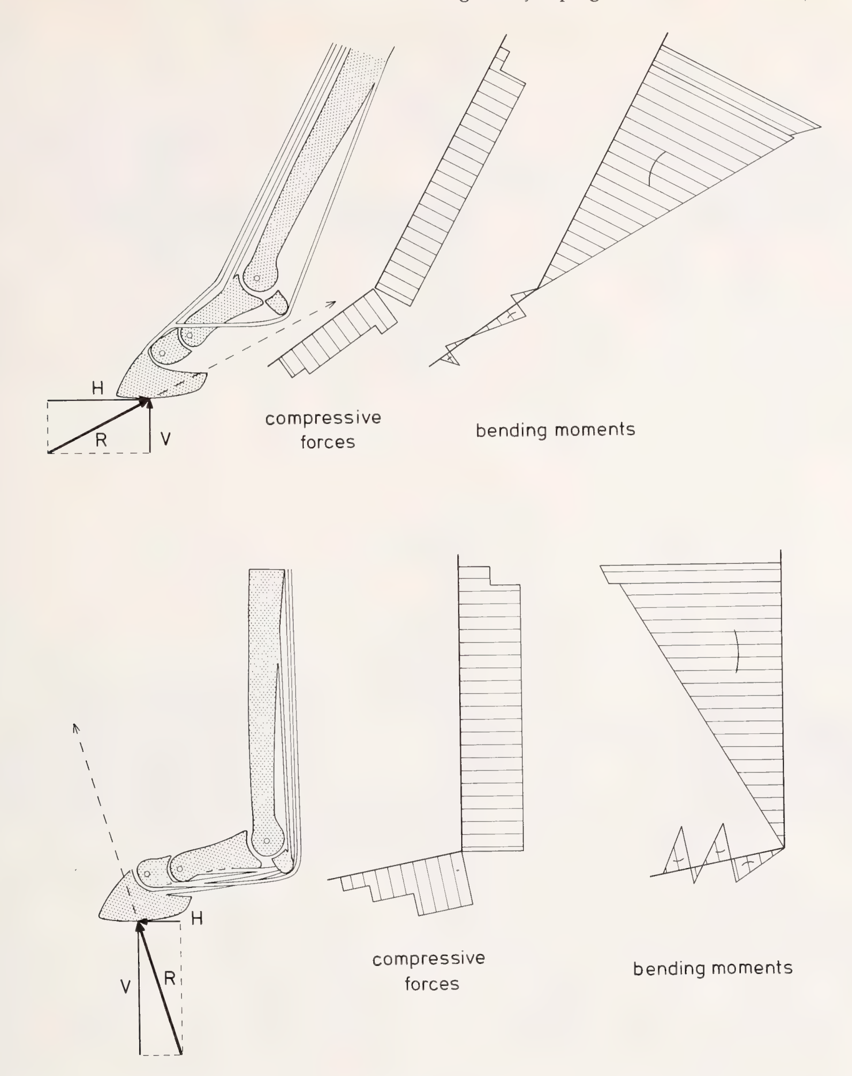


Fig. 4. Two examples to illustrate the external forces acting on a hoof. The positions of the skeletal elements and the tendons are shown, along with the respective stress patterns.
Top: early braking, hindfoot, bottom: post midstance, propelling

of the gait. In turn, the contact times, as well as the intervals of load-bearing, decrease with speed. The widths of the hoof seem to be proportional to ground-foot forces. At least these oscillograms are similar to our force plate measurements. The harder the ground, the higher the ground-foot forces, and the shorter the time of force exchange.

The period during which loads are transmitted to the ground (interval of weight-bearing) is by 0.08 s (walk), 0,06 s (trot) and 0,05 s (gallop) shorter than the electronically measured ground contact (= stance duration). The same result was obtained by comparing slow motion films with measurements, or force plate recordings.

We conclude that the animal controls and adapts the forces exchanged between body and ground to compensate for disturbances and imbalances, but avoids variation in time. By doing so it can take advantage of elastic resilience of its tendons (Dawson and Taylor

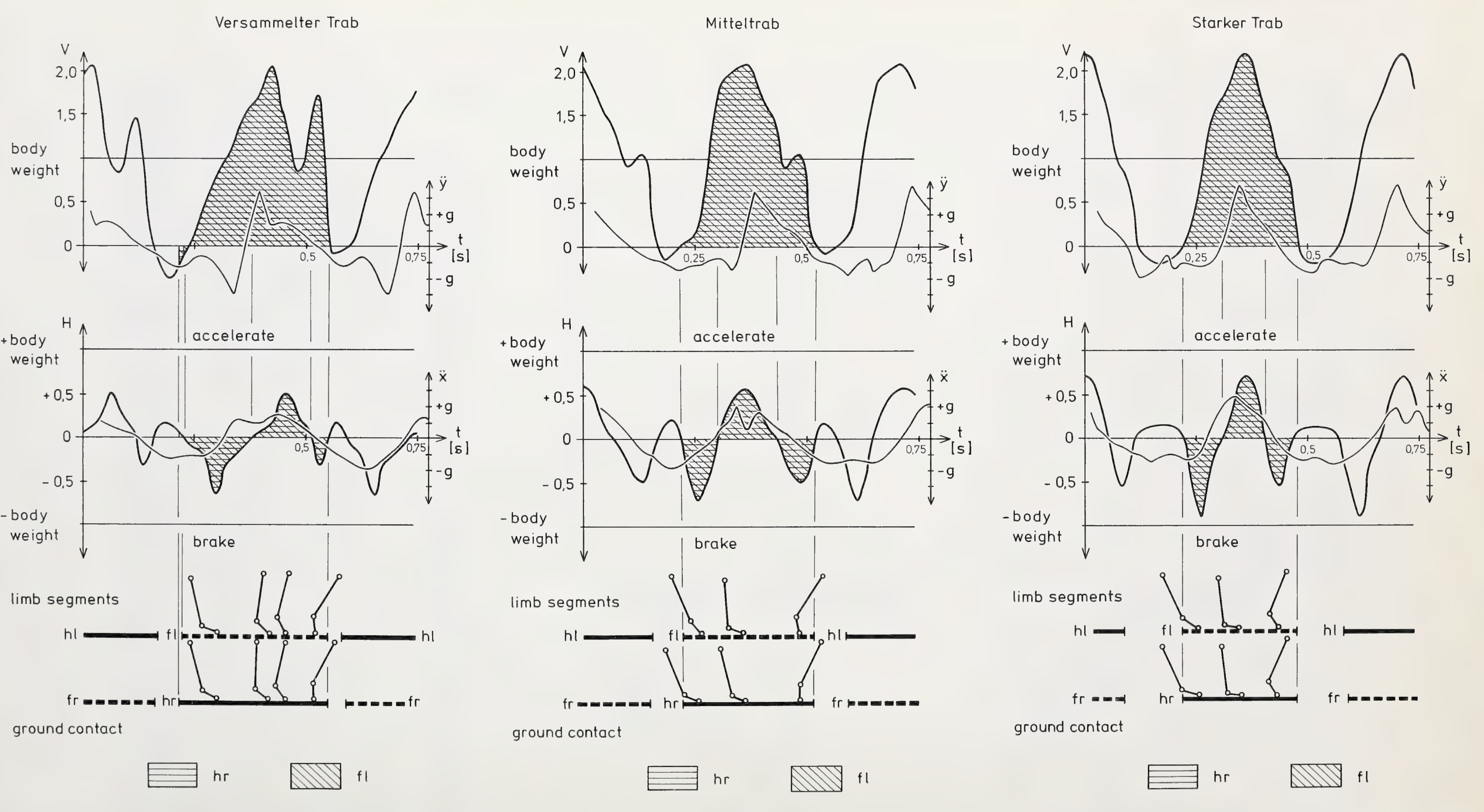


Fig. 5. Forces acting against the body of the horse trotting in 3 "tempi" (= speeds). Top row: vertical forces over time. Scales are given on left side. On the same time axis as base line, the recording of the accelerometer is shown, scale on right side. The hatching indicates support of the body by individual hooves. Middle row: braking (−) and propelling (+) on same time scale. Bottom row: the timing of footfalls and contact intervals (= stance duration). h = hind, f = front, r = right, l = left. The actual positions of the foot in critical phases of the stance period are shown as stick figures

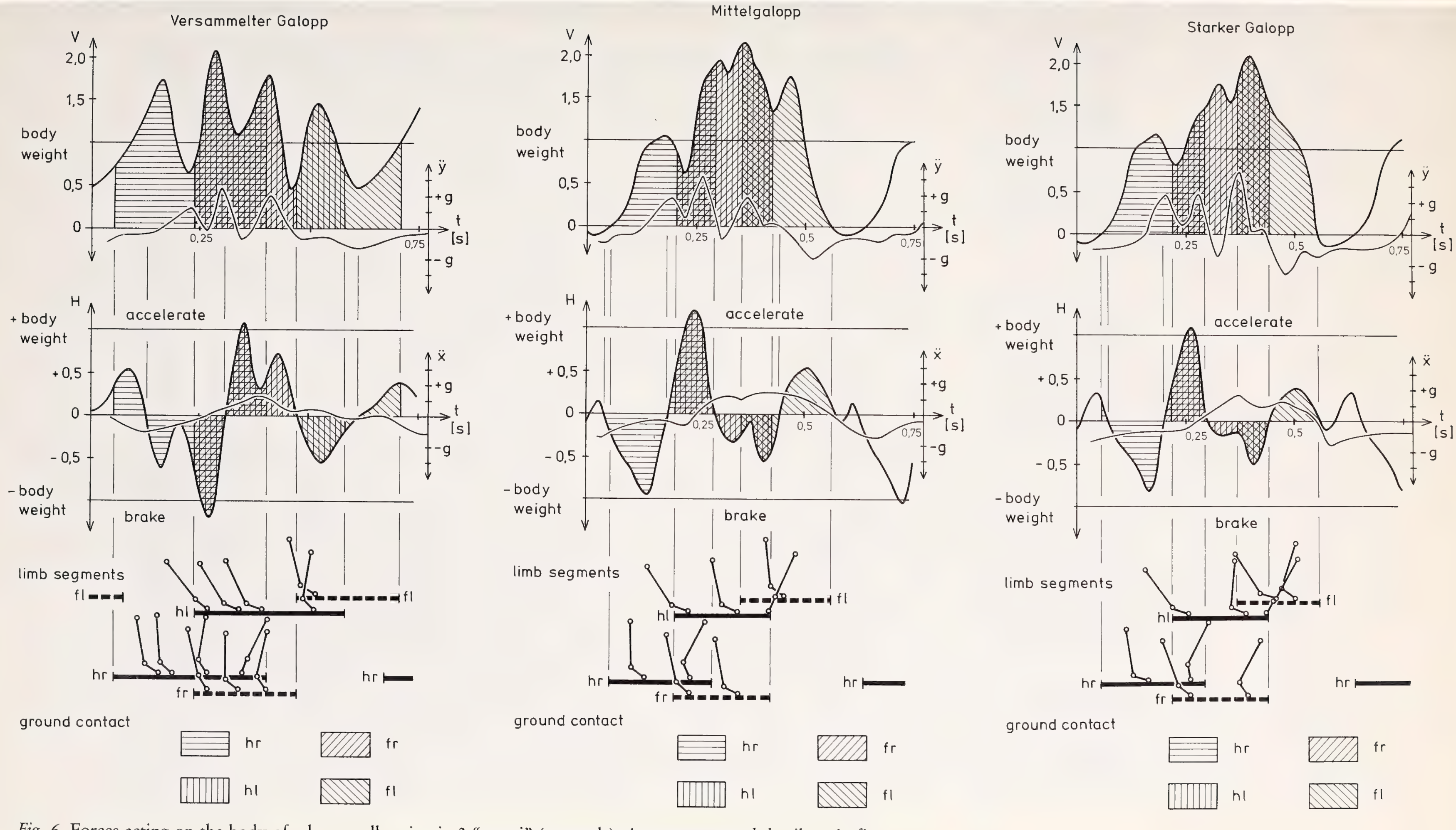


Fig. 6. Forces acting on the body of a horse gallopping in 3 "tempi" (= speeds). Arrangement and details as in fig. 5

1973; Ker 1985), which is primarily a function of time. This gives support to all ideas which interprete the locomotion of cursorial animals as a spring mechanism based on the elastic resilience of their long tendons. (Dawson and Taylor 1973; Taylor 1978; Alexander 1982, 1984, 1985; MacMahon 1984; Dimery and Alexander 1985; Hildebrand 1985).

The total forces acting on the body of the horse have been calculated for various „tempi" of the trot (fig. 5). The (larger) vertical components amount up to 2.11 times body weight (starker Trab). The calculated values coincide reasonably with the measured accelerations.

The rotations of the trunk axis indicate that in phases of support by a front- and a hindlimb ⅓ (at low speed) to ½ (at high speed) of this maximal force is carried by the hindlimb. This corresponds to the weight distribution in standing and force distribution during walking in other cursorial animals (Kimura et al. 1979). These results are also in line with fig. 7: The horizontal distances from the foot on ground to the body's center of gravity are much longer in the hindlimbs than in frontlimbs. Because of the external equilibrium, a larger share of body weight must be carried on the frontlimbs (see also riding instructions, e. g. Podhajsky 1968).

The smaller sagittal forces split into braking and propelling components. The braking forces act at the onset of the stance phase and reach higher values than afterwards. In or shortly after the middle of the stance phase, they change their sign and reach a positive maximum of 0.5 or 0.7 body weight.

At the end of the stance phase, there is a depression in the vertical, and a negative value of the sagittal force components. In these features, our results deviate from recordings of the ground reactions in horses (Biewener et al. 1983) and in other mammals (Kimura et al. 1979), in which the sagittal components use to stay at a lower level until the stance period is over, while the vertical forces do not show the ditch in their last sections.

This seems to be a consequence of the procedure we employed, namely summation of forces: At the end of the stance phase, the supporting limbs are lifted from the ground and accelerated foreward, thus exerting a "drag" on the continuously moving rest of the body.

The forces which come into action in the gallopping horse are shown in fig. 6. The vertical components can easily be interpreted as the superposition of the ground contacts of the individual feet. As in the trot, the maxima are 2–2.1 times body weight. The calculated forces agree reasonably with the measured accelerations.

The horizontal forces indicate a braking by the trailing hindlimb, which touches down first, and possibly by the diagonal hind- and frontlimb put down synchronously. Propulsion takes place immediately after the diagonal footfall, is interrupted by a second braking period which coincides with lift-off of the diagonal and touchdown of the last (leading) frontlimb. Propulsion is resumed when the body swings over the leading frontlimb. These forces do not agree with the pattern of sagittal accelerations measured at the saddle. The latter is negative until the diagonal front- and hindlimbs are put on the ground, then it becomes positive, changing its sign again during mid-stance phase of the leading frontlimb. This is the pattern of ground reaction forces which has been measured in horses (Biewener et al. 1983), smaller ungulates, monkeys and dogs (Kimura et al. 1979).

The difference between measured accelerations and calculated forces may either be due to vibrations of the saddle against the trunk or once more a consequence of the calculating procedure we have used.

The maximal forces of front- and hindlimbs are not reached at the same time. The vertical ground reactions transmitted through the frontlimbs are usually 1.4 or 2.2 times higher than those on the hindlimbs – a relationship similar to that reported above for two-limb supports in the trot.

The contact times found in the film analyses and used for these calculations differ slightly from those measured in other, less well trained horses.

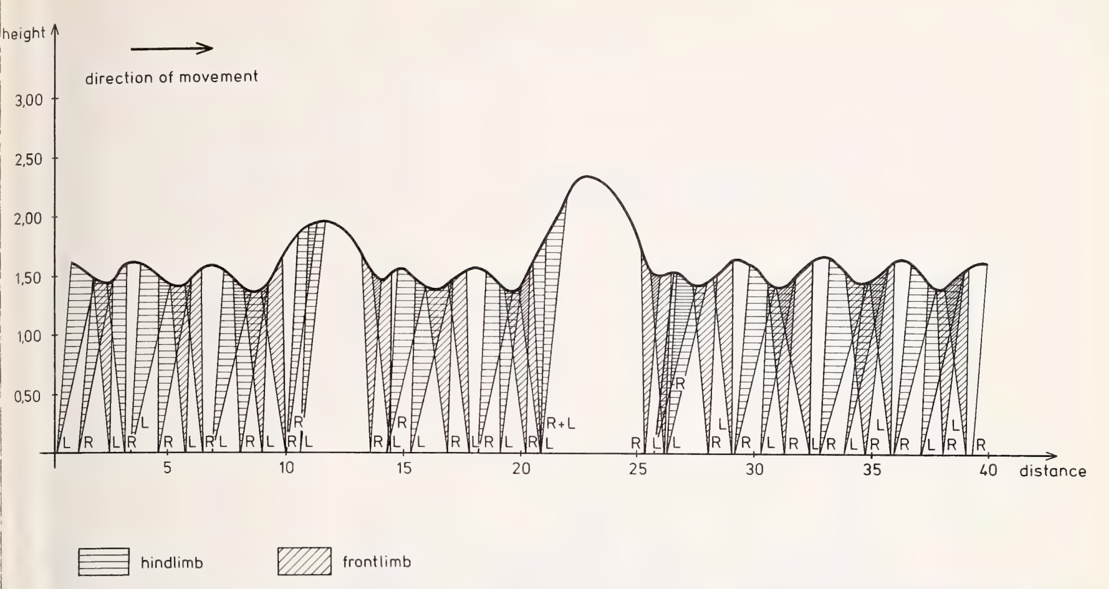


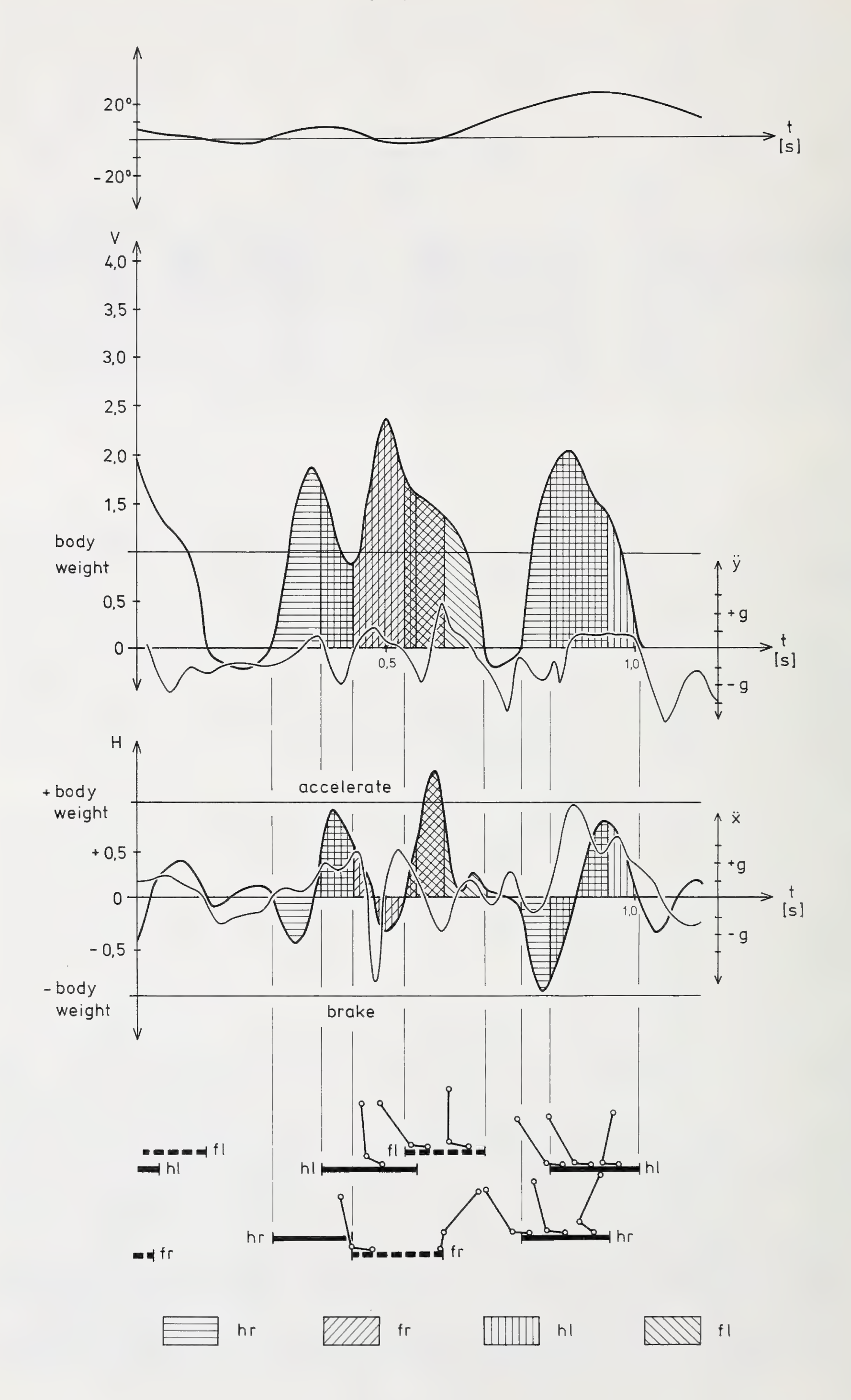
Fig. 7. Movements of a point at the saddle over support limbs. Gallop and combination of two obstacles as an example. The positions of the saddle point at touchdown and at lift-off of each limb are connected with the footing hoof. The covered angles are hatched, to show the distances over which the body travels during the stance period of a given limb

According to various parameters (Preuschoft et al. 1987), two sorts of jumps could be discriminated: high (regardless of the obstacle) and wide (over moats), (figs. 8, 9). Even in high jumps over 1.55 m, the center of gravity is lifted only 0.8 m to 0.9 m above its height in the standing horse. The apex of its trajectory is passed in jumps less than 1.20 m high before the hindlimbs lose ground contact (fig. 7). The contact intervals of the various limbs are so coordinated, that the accelerations or decelerations are distributed over all 4 extremities, and kept at a rather moderate level.

In the take-off for a broad jump (fig. 8), we find a usual gallop cycle with a vertical component going up to 2.4 body weight, that is more than in cycles on the flat. Magnitude and arrangement in time of sagittal forces are most similar to the fastest gallop, except that the frontlimbs produce more foreward propulsion. After a short phase of suspension, both hindlimbs are planted on the ground simultaneously, and exert high vertical, as well as braking, and later propelling forces.

In the high jump (fig. 9), the gallop cycle is compressed to last only 0.3 instead of 0.6 s, so that the peaks are completely fused to one hump of less than 2 times body weight. The sagittal components are as before. After a short suspension of 0.03 s the hindlimbs hit the ground, with 2.2 times body weight in the vertical, a strong braking and a smaller, though still high propelling component. In essential the same biphasic pattern of external forces has been recorded on a force plate by Alexander (1974) for a jumping dog, and by Günther et al. (1987) for a jumping Japanese macaque. Remarkable is the shortness of the take-off. We know from other leapers that a short take-off correlates with height or width (Preuschoft et al. 1979; Peters and Preuschoft 1984; Günther 1985; Günther et al. 1987). In all cases, the measured accelerations are in principal accordance with the calculated forces.

The landing is extended over more than 0.5 s. Having crossed the moat, the horse puts down one (the trailing), 0.05 s later the second (leading) frontlimb. The vertical component is less than 2 times body weight, the braking components are very high (1.0 in the first and 1,2 times body weight in the second frontlimb). The hindlimb contacts are separated by a


broad jump (take-off)
20°
-20°
t
[s]
V
4,0
3,5
3,0
2,5
2,0
1,5
body
weight
0,5
0
0,5
1,0
ÿ
+g
-g
H
+ body
weight
accelerate
+ 0,5
0
- 0,5
- body
weight
brake
ẍ
fl
hl
hr
fr
hr
fr
hl
fl

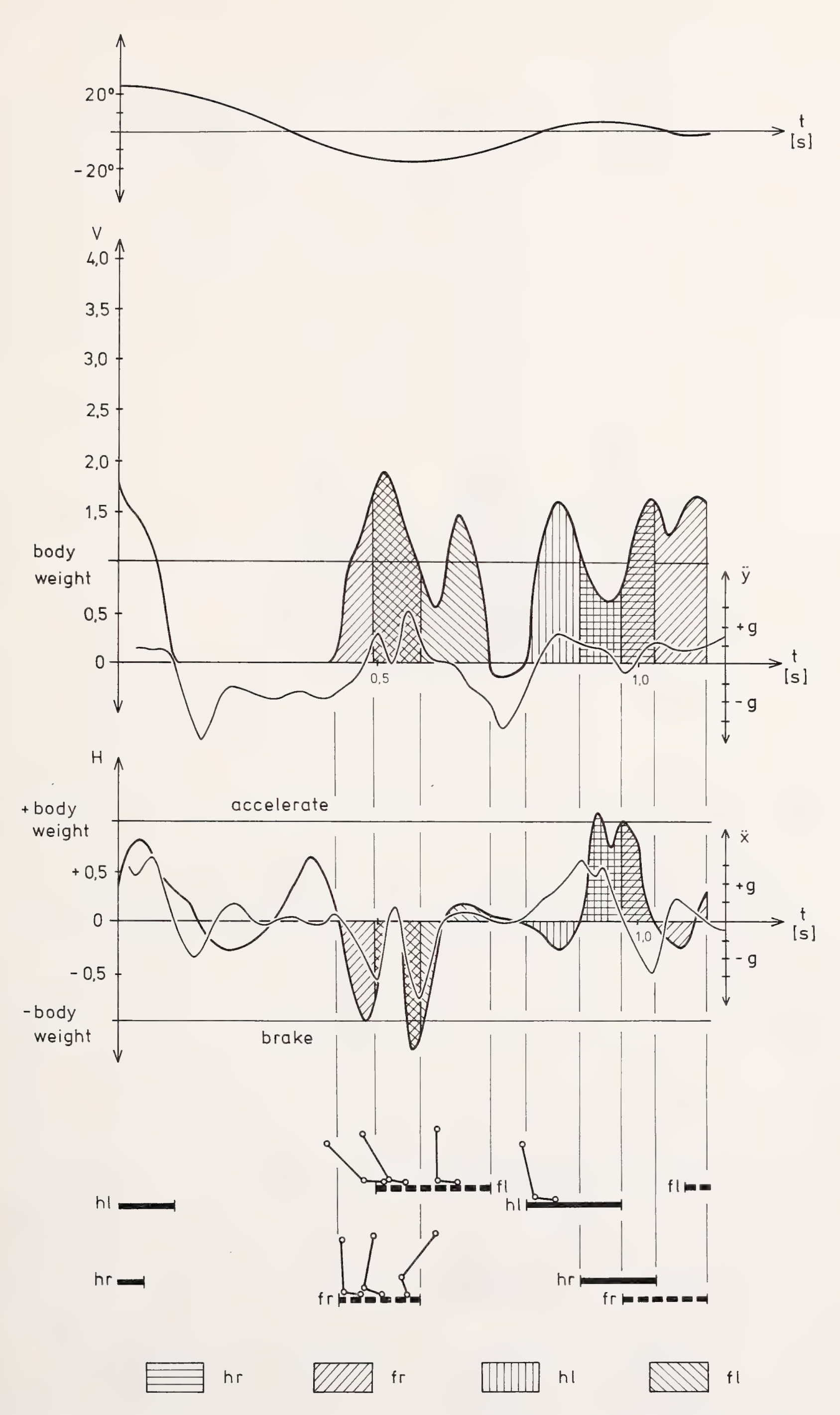
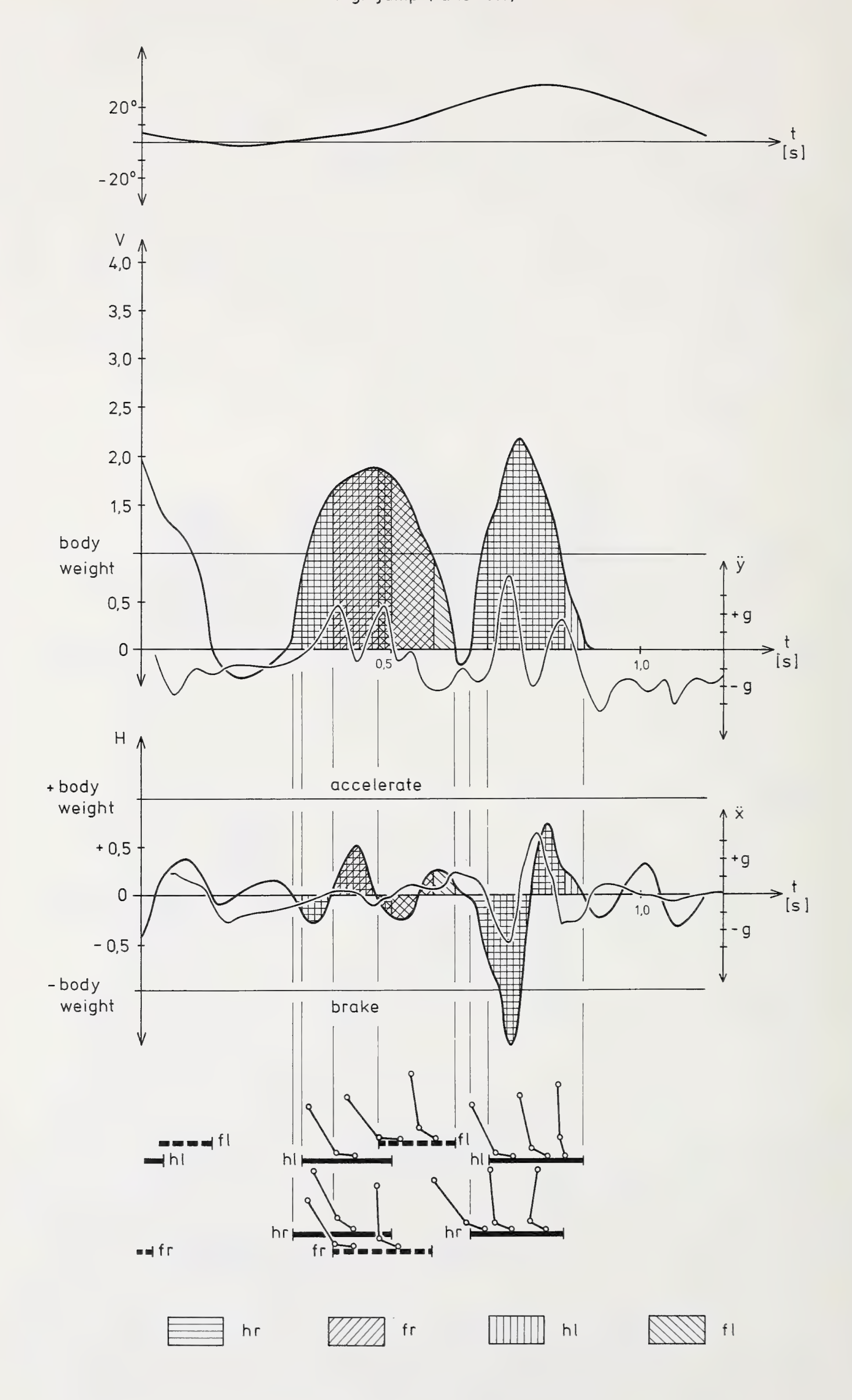


Fig. 8. Forces acting on the body of a horse in a broad jump. Arrangement and details as in fig. 9


high jump (take-off)
20°
-20°
t
[s]
V
4,0
3,5
3,0
2,5
2,0
1,5
body
weight
0,5
0
0,5
1,0
ÿ
+g
-g
H
+body
weight
accelerate
+0,5
0
-0,5
-body
weight
brake
ẍ
fl
hl
hr
fr
hr
fr
hl
fl

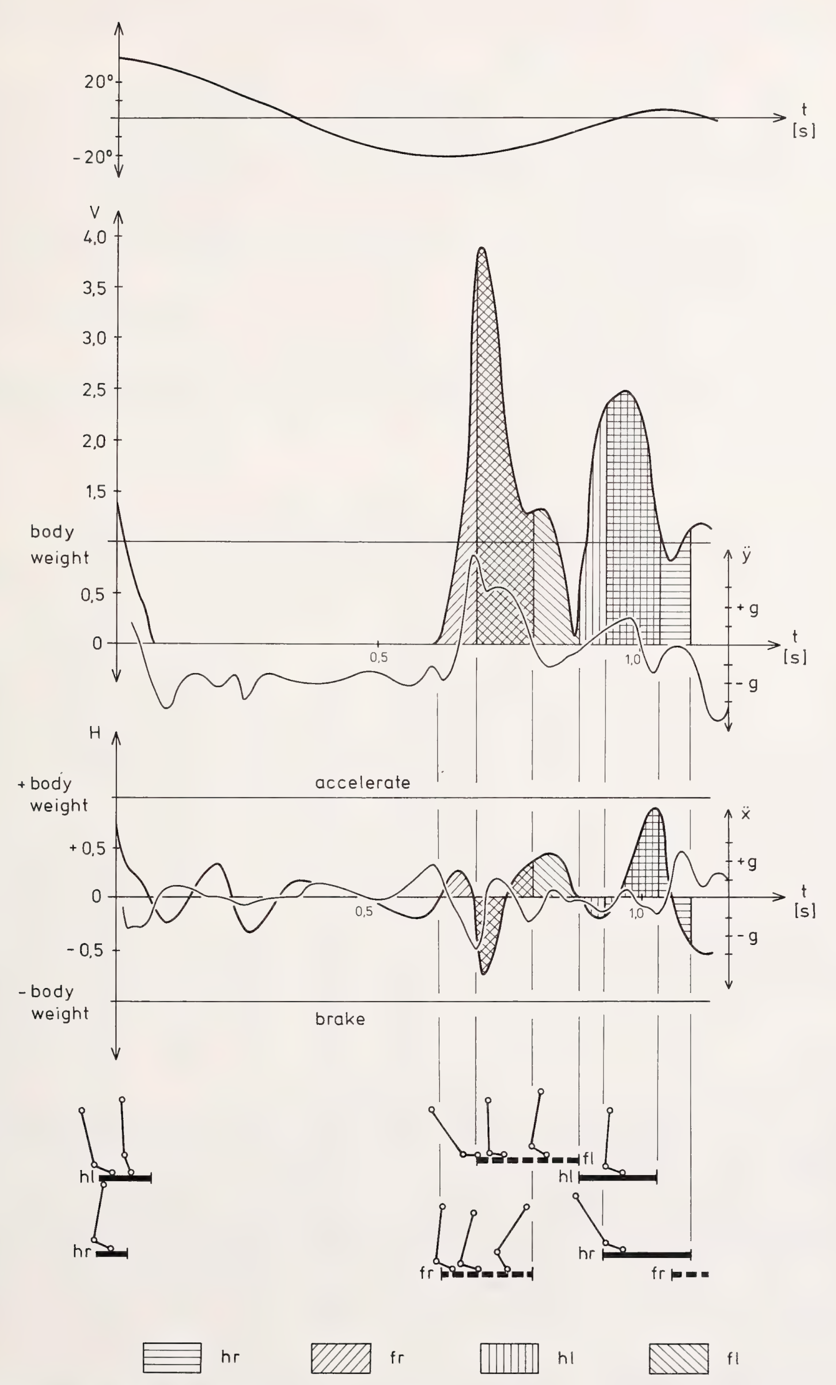


Fig. 9. Forces acting on the body of a horse in a high jump. Top row: Inclination of trunk axis. Second row: vertical forces over time. Scales are given on left side. On the same time axis as base line, the recording of the accelerometer is shown, scale on right side. The hatching indicates support of the body by individual hooves. Third row: braking (−) and propelling forces (+) in horizontal direction on same time scale. Bottom row: the timing of footfalls and contact intervals. h = hind, f = front, r = right, l = left. The actual positions of the foot in critical phases of the stance period are shown as stick figures

phase of suspension of 0.01 from ground contact of the frontlimbs, and the first pushes the body upward – just stopping tail down rotation – and then exerts, together with the second, high propulsory forces (1.1 and 1.0 times body weight). These processes are reflected in the measured accelerations.

Landings after high jumps differ from this pattern. The first (trailing) and the second (leading) frontlimb are spaced in time by 0.07 s, the vertical force transmitted being 3.85 and the braking component 0.8 body weight. In the later part of the two-limb stance, there is a reacceleration. The first (trailing) hindlimb touches down before or shortly after frontlimb lift-off, the second (leading) follows 0.05 s later. Both hindlimbs transmit another 2.4 times body weight in the vertical. While braking is minor, a forward thrust by 0.85 times body weight is produced. Again the measured accelerations coincide largely with the calculated forces.

The hooves on the ground are the only points at which external forces can be applied to the horse's body. So a combination of the calculated vertical and horizontal forces should be equivalent to the external forces acting on the hooves.

Even in the landing the damping mechanisms are so effective, that the increase of force is slow enough to exclude kinetic stress patterns, or shock waves in parts of the locomotor apparatus (PREUSCHOFT 1985).

Table 3. **Maximal stresses found by calculation in the feet of horses** $\left[\frac{\text{kp}}{\text{cm}^2}\right]$

	Front				Hind			
Gait, tempo	Compression fetlock joint	Compression metacarpal	Bending stress proximal section of metacarpal	Total stresses	Compression fetlock joint	Compression metatarsal	Bending stress proximal section of metatarsal	Total stresses
"Versammelter Trab"	420	854	1406	1920	211	430	527	957
			−2145	−1631			−587	−157
"Mitteltrab"	397	808	2772	3580	407	830	2575	3405
			−1816	−1008			−2870	−2040
"Starker Trab"	418	850	2990	3840	421	857	2597	3454
			−2855	−2296			−2894	−2037
"Versammelter Galopp"	367	747	2350	2832	493	1003	2250	2770
			−1540	−1058			−2507	−1987
"Mittelgalopp"	332	676	2216	2892	482	980	2494	3474
			−1452	−1630			−2786	−1806
"Starker Galopp"	390	794	2210	3004	433	881	2322	3203
			−1447	−1850			−2588	−1850
Wide jump	414	843	2414	2920	592	1204	2520	3201
(moat) take-off			−1581	−1195			−2808	−2308
High jump	278	565	2263	2828	462	940	2298	2885
(simple bar)			−1483	− 918			−2561	−2049
take-off								
Wide jump	646	1313	2264	2841	518	1053	1780	2746
(moat) landing			−2332	−1320			−1887	− 834
High jump	817	1662	2002	2868	475	966	2571	3066
(simple bar)			−1312	−1565			−2867	−2372
landing								

+: compression; −: tension

For a number of phases in which the direction of the external ground-foot force is beyond reasonable doubt, we have calculated the internal forces and stresses. Out of the 84 calculations made, table 3 shows the highest values for each gait or type of jump.

Conclusions

In horses, the angles of excursion during stance phase are rather acute (MacMahon 1984; Hildebrand 1985), that means they are kept more or less in line with the large perpendicular component of the reaction force.

The decrease of the braking, and the increase of the accelerating component coincides with the swing of the extremity from anteversion to retroversion. This is a means to relieve the limbs from too great bending moments. In most cases, the compressed side of the bent foot is in front, at the side of the compression-resistent metapodial or phalanx. The extended side of the foot is at the rear, where the tendons and the interosseous medius form strong ties. Preuschoft and Fritz (1977), found that bending moments are greater in the more resistent hind- than in the less strong frontlimbs. The rudimentary second and fourth rays contribute considerably to the bending strenght of the metapodial segment. In most cases the sense of bending is foreward concave. These results are confirmed. Nonetheless, most movements imply a change of the sense of bending the metapodial.

In usual gaits of still moderate speed which are considered by riding instructions (e.g. Podhajsky 1968) as "natural locomotion" of horses, stresses reach surprisingly high values. These are hardly exceeded by the stresses found in jumps. This observation is in agreement with our recordings of accelerations, which do never show the high force peaks we calculated for landings.

Horses possess the ability to distribute the take off and the landing over long periods and over all 4 limbs, so that the stresses inside the limbs are kept within reasonable limits. Very high stresses do not only occur in jumping, but in faster dressage gaits as well.

The calculated stresses are far beyond the experimentally observed strength properties of bones. This seems to depend on our calculations, which assumed a linear increase of stresses on the cross section – an assumption which does not seem to hold true in view of recent observations on bone microstructure (Amtmann 1971; Yamada 1973; Doden 1987), although Cheney et al. (1973) have also found breaking stresses in the size order of our calculations.

In spite of this, our results show that and why a suboptimal coordination of movements, particularly in jumping horses, may become fatal: If the distal limb segments are not placed perfectly parallel to the direction of the external force, the bending stresses assume rapidly very high values which exceed the strength of the tissues.

Acknowledgements

This study was supported by the Ministerium für Wissenschaft und Forschung des Landes Nordrhein-Westfalen, Deutsche Forschungsgemeinschaft, and Reiterliche Vereinigung, Warendorf. I also wish to thank the owners and institutions mentioned in this paper for their active support and encouragement given to our work, as well as for their patience in waiting for the results. Dr. M. Fritz made the calculations, U. Nieschalk, I. Streitlein, D. Kapretz, D. Becker, K. Albert, M. Günther have contributed to the evaluation of the raw data. M. Wischniwetzki and H. Schulze have drawn the figures and H. Schepers has typed the manuscript. Without their help, the work would never have been carried out.

Zusammenfassung

Die äußeren Kräfte und die inneren Spannungen im „Fuß" von Dressur- und Springpferden

Ziel der Untersuchung ist die Ermittlung der für die Anpassung der Körperform maßgeblichen Variablen der Bewegungsabläufe. Als Beispiel für spezialisierte Läufer unter den Säugern haben wir Pferde ausgewählt. Filmaufnahmen mit 200 B/s aus konstanter Entfernung dienten zur Vermessung der Bewegungen von Gelenken und den dazwischen liegenden Segmenten in Dressurgangarten und Sprüngen unter dem Reiter. Anhand mehrerer einfacher Parameter haben wir die Variabilität der Bewegungsabläufe abgeschätzt. Die zeitlichen Verläufe und die Trittlängen haben sich als bemerkenswert konstant erwiesen, ebenso wie die Bewegungsabläufe beim Springen. Die Kräfte zwischen Huf und Boden hingegen variieren von Tritt zu Tritt beträchtlich. Die Geschwindigkeiten und Beschleunigungen des ganzen Körpers und seiner Teile wurden dann für durchschnittliche Bewegungszyklen errechnet. Unter Benutzung von Segmentgewichten, die der Literatur entnommen wurden, ließen sich die „äußeren" Kräfte bestimmen. Die so erzielten Ergebnisse stimmen recht gut mit Beschleunigungen und Reaktionskräften überein, die wir direkt gemessen haben. Die Kräfte, die zwischen dem Körper des Pferdes und dem Boden ausgetauscht werden, sind meist zweimal, manchmal fast viermal so hoch wie das Körpergewicht. Diese Kräfte werden auf mehrere Extremitäten und über längere Zeitintervalle verteilt. Die Reaktionskräfte, die beim Start vor und bei der Landung nach einem Sprung auf eine einzelne Extremität wirken, sind in der gleichen Größenordnung wie die Reaktionskräfte im „starken Trab" oder im „starken Galopp". Beide führen zu Spannungen von kritischer Höhe, insbesondere wenn die distalen Extremitäten-Abschnitte nicht in optimale Positionen gebracht werden können.

References

Alexander, R. McN. (1974): The mechanics of jumping by a dog *(Canis familiaris).* J. Zool., London, **173,** 549–573.

— (1982): Locomotion of animals. Glasgow: Blackie.

— (1984): Elastic energy stores in running vertebrates. Am. J. Zool. **24,** 85–94.

Alexander, R. McN.; Dimery, N. J. (1985): Elastic properties of the fore foot of the donkey, *Equus asinus.* J. Zool. (London) **205,** 511–524.

Alexander, R. McN.; Jayes, A. S.; Maloiy, G. M. O.; Wathuta, E. M. (1979): Allometry of the limb bones of mammals from shrews *(Sorex)* to elephant *(Loxodonta).* J. Zool. London, **189,** 305–314.

Amtmann, E. (1971): Mechanical stress, functional adaptation and the variation structure of the human femur diaphysis. Ergeb. Anat. Entw. Gesch. **44,** 1–89.

— (1979): Biomechanical interpretation of form and structure of bones: role of genetics and function in growth and remodeling. In: Environment, Behavior and Morphology: Dynamic Interactions in Primates. Ed. by M. E. Morbeck, H. Preuschoft and N. Gomberg. New York: G. Fischer. 183–208.

Bayer, A. (1973): Bewegungsanalysen an Trabrennpferden mit Hilfe der Ungulographie. Zbl. Vet. Med. **20,** 209–221.

Biewener, A. A.; Thomason, J.; Goodship, A.; Lanyon, L. E. (1983): Bone stress in the horse forelimb during locomotion at different gaits: A comparison of two experimental methods. J. Biomechanics **16,** 565–576.

Cartmill, M. (1974): Pads and claws in arboreal locomotion. In: Primate Locomotion. Ed. by F. Jenkins. New York: Acad. Press, 45–83.

Cheney, J. A.; Liou, S. Y.; Wheat, J. D. (1973): Cannon-bone fracture in the thoroughbred racehorse. Med. Biol. Eng. **11,** 613–620.

Dawson, T. J.; Taylor, C. R. (1973): Energetic cost of locomotion in kangaroos. Nature **246,** 313–314.

Demes, B.; Günther, M. M. (1987): Einfluß der Masse auf die Körperproportionen und den Bewegungsablauf von springenden Halbaffen. Z. Säugetierkunde., Sonderbd. zur 61. Vers. d. Ges. f. Säugetierkde., p. 13 (abstract only).

Demes, B.; Günther, M. M. (1988): Wie die Körpermasse den Springstil von Halbaffen und deren Proportionen bestimmt. Z. Morph. Anthrop. (in press).

Demes, B.; Jungers, W. L.; Nieschalk, U. (1988): Size- and speed-related aspects of quadrupedal walking in slender and slow lorises. In: Gravity in Primates. Ed. by F. K. Jouffroy and C. Niemitz. Firenze: Il Sedecesimo (in press).

Dimery, N. J.; Alexander, R. McN. (1985): Elastic properties of the hind foot of the donkey, *Equus asinus.* J. Zool., London, (in press).

Doden, E. (1987): Zur strukturellen Variation der langen Skeletelemente der Hand als Greif- und/ oder Lokomotionsorgan. Verh. Anat. Ges. **81,** 253–269.

Günther, M. M. (1985): Biomechanische Voraussetzungen beim Absprung des Senegalgalagos. Z. Morph. Anthrop. **75**, 287–306.
Günther, M. M.; Ishida, H.; Ohta, M.; Kumakura, S. (1987): Behavioural adaptations towards reduction of external stresses acting on the locomotor apparatus during rapid movements, and the impact created by the take-off and landing in leaping primates. In: Gravity in Primates. Ed. by F. K. Jouffroy and C. Niemitz. Firenze: Il Sedecesimo (in press).
Hildebrand, M. (1985): Walking and running. In: Functional Vertebrate Morphology. Ed. by M. Hildebrand, D. M. Bramble, K. F. Liem and D. B. Wake. Cambridge, London: Harvard University Press, 38–57.
Hoyt, D. F.; Taylor, C. R. (1981): Gait and the energetics of locomotion in horses. Nature **292**, 239–240.
Jungers, W. L. (1984): Aspects of size and scaling in primate biology with special reference to the locomotor skeleton. Yb. Phys. Anthrop. **27**, 73–97.
— (1985): Body size and scaling of limb proportions in primates. In: Size and Scaling in Primate Biology. Ed. by W. L. Jungers. New York: Plenum Press, 345–381.
Ker, R. F. (1985): Elasticity of hand and forefoot tendons. In: "Hands". Ed. by. H. Preuschoft and D. J. Chivers (in press).
Kimura, T.; Okada, M.; Ishida, H. (1979): Kinesiological characteristics of primate walking: Its significance in human walking. In: Environment, Behavior and Morphology: Dynamic Interactions in Primates. Ed. by M. E. Morbeck, H. Preuschoft and N. Gomberg. New York: G. Fischer. 297–311.
Kummer, B. (1959): Bauprinzipien des Säugerskeletes. Stuttgart: Thieme.
McMahon, Th. A. (1984): Muscles, Reflexes, and Locomotion. Princeton, New Jersey: Princeton University Press.
Oxnard, C. E. (1979): The morphological-behavioral interface in extant primates: some implications for systematics and evolution. In: Environment, Behavior and Morphology: Dynamic Interactions in Primates. Ed. by M. E. Morbeck, H. Preuschoft and N. Gomberg. New York: G. Fischer. 183–208.
Pauwels, F. (1965): Gesammelte Abhandlungen zur funktionellen Anatomie des Bewegungsapparates. Heidelberg, Berlin: Springer.
Peters, A.; Preuschoft, H. (1984): External biomechanics of leaping in *Tarsius* and its morphological and kinematic consequences. In: Biology of Tarsiers. Ed. by C. Niemitz. Stuttgart: G. Fischer, 227–255.
Plagenhoef, St. (1979): Dynamics of human and animal motion. In: Environment, Behavior and Morphology: Dynamic Interactions in Primates. Ed. by M. E. Morbeck, H. Preuschoft and N. Gomberg. New Yorker: G. Fischer. 277–296.
Podhajský, A. (1968): Kleine Reitlehre. München: Nymphenburger Verlagsbuchhandlung.
Preuschoft, H. (1969): Statische Untersuchungen am Fuß der Primaten. I. Phalangen und Metatarsalia. Z. Anat. Entw. Gesch. **129**, 285–345.
— (1970a): Functional anatomy of the lower extremity. In: The Chimpanzee. Ed. by G. H. Bourne, Basel, München and New York: Karger. Vol. **3**, 221–294.
— (1970b): Statische Untersuchungen am Fuß der Primaten. II. Statik des ganzen Fußes. Z. Anat. Entwickl. Gesch. **131**, 156–192.
— (1973): Functional anatomy of the upper extremity. In: The Chimpanzee. Ed. by G. H. Bourne. Basel, München and New York: Karger. Vol. **6**, 34–120.
— (1979): Motor behavior and shape of the locomotor apparatus. In: Environment, Behavior and Morphology: Dynamic Interactions in Primates. Ed. by M. E. Morbeck, H. Preuschoft and N. Gomberg. New York: G. Fischer. 263–275.
— (1985): On the quality and magnitude of mechanical stresses in the locomotor system during rapid movements. Z. Morph. Anthrop. **75**, 245–262.
— (1988): Biomechanical approach to the evolution of the facial skeleton of hominoid primates. Fortschr. d. Zool. Stuttgart: G. Fischer (in press).
Preuschoft, H.; Demes, B. (1984): Biomechanics of brachiation. In: The Lesser Apes. Ed. by H. Preuschoft, W. Y. Brockelman, D. J. Chivers and N. Creel. Edinburgh University Press. 96–118.
— (1985): Influence of size and proportions on biomechanics of brachiation. In: Size and Scaling in Primate Biology. Ed. by W. L. Jungers. New York: Plenum-Press. 383–398.
Preuschoft, H.; Fritz, M. (1977): Mechanische Beanspruchung im Bewegungsapparat von Springpferden. Fortschr. d. Zool. **24**, 75–98.
Preuschoft, H.; Fritz, M.; Niemitz, C. (1979): The biomechanics of the trunk in primates and problems of leaping in Tarsius. In: Environment, Behavior and Morphology: Dynamic Interactions in Primates. Ed. by M. E. Morbeck, H. Preuschoft and N. Gomberg. New York: G. Fischer, 327–345.

Preuschoft, H.; Knisel, G.; Fritz, M. (1987): Die Bewegungen von Pferden beim Springen. Warendorf: FN-Verlag, Wissenschaftl. Publikation **9**, 60–119.
Preuschoft, H.; Streitlein, I. (1987): Die Kinematik der Trabtempi bei Reitpferden. Warendorf: FN-Verlag, Wissenschaftl. Publikation **9**, 20–59.
Taylor, C. R. (1978): Why change gaits? Recruitment of muscles and muscle fibers as a function of speed and gait. Amer. Zool. **18**, 153–161.
Yamada, H. (1973): Strength of biological materials. Huntington, New York: R. E. Krieger.

Author's address: Prof. Dr. H. Preuschoft, Funktionelle Morphologie, Anatomisches Insitut, Ruhr-Universität Bochum, D-4630 Bochum 1, FRG

BUCHBESPRECHUNGEN

RÖHRS, M.; MEYER, H. (Hrsg.): **Studium Generale.** Vorträge zum Thema „Mensch und Tier". Band V. Hannover: M. & H. Schaper 1987/88. 108 pp. DM 18,–. ISBN 3-7944-0156-5

Der neue (5.) Band der Vorträge des Studium Generale an der Tierärztlichen Hochschule Hannover enthält drei kulturgeschichtlich-volkskundliche Vorträge zum Thema „Das Tier in der Literatur und in der Kunst". ARENDT („Der Fuchs war ein Jurist vom Fach") und RÖLLEKE („Das Tier in Grimms Märchen") besprechen das Tier in Märchen, Fabeln und Legenden. WERNER behandelt „Natur- und Symbolbedeutung des Tieres in der bildenden Kunst von der Vorgeschichte bis zur frühen Neuzeit". Zwei weitere Beiträge dürften für den Säugetierkundler von besonderem Interesse sein: D. VON HOLST bietet eine umfassende, kritisch abgewogene Zusammenfassung zum Thema „Sozialer Stress bei Tier und Mensch" und damit eine sehr informative Übersicht über den Stand dieses aktuellen Problems; DITTRICH bietet einen historischen Beitrag zum Thema „Wildtiere in menschlicher Obhut, vom Mittelalter bis zum 19. Jahrhundert". Im Mittelpunkt der Darstellung stehen nicht die zoologischen Gärten, sondern die bisher kaum behandelten Berichte über höfische und private Tierhaltung, Tierhaltung für Kampfspiele und wandernde Tierschauen.

Die Beiträge wenden sich an ein größeres Publikum und bieten dem Interessierten zu den genannten Themen solide Informationen in angemessener Form und auf gutem Niveau.

D. STARCK, Frankfurt/M.

LANGER, P.: **The Mammalian Herbivore Stomach.** Comparative Anatomy, Function and Evolution. Stuttgart, New York: Verlag Gustav Fischer 1988. 557 pp., 245 figs., 72 tables. DM 248,–. ISBN 3-437-30568-9

Das vorliegende Werk ist ein Musterbeispiel dafür, was eine moderne, funktionell und evolutionsbiologisch orientierte Morphologie, die offen ist für interdisziplinäre Methoden und Problemlösungen, zu leisten vermag. Der Autor bemüht sich, nicht nur die Basis an Fakten zu erweitern und zu vertiefen, sondern versteht in höchst gelungener Weise, das komplexe Netz von morphogenetisch wirksamen Faktoren zu entwirren und verständlich zu machen. Ergebnisse der Physiologie, der Stammesgeschichte und Palaeontologie, der Ökologie werden dabei ebenso berücksichtigt wie tiergeographische, vegetationskundliche und ernährungsbiologische Befunde.

Das Buch bietet eine umfangreiche und subtile vergleichende Bearbeitung des multilokulären Magens der Paarhufer, Sirenen, Faultiere, Blätteraffen (Colobidae) und Känguruhs (Potoroinae und Macropodinae). Behandelt werden außer der makromorphologischen Form und Topographie jeweils Kompartimentierung, Verhalten der Muskulatur, Gefäße, Epithelien, Innervation und ontogenetische Entwicklung. Besondere Aufmerksamkeit ist der Motilität und deren Regulation (Falten, Klappen, Taenien etc.) gewidmet. In diesem Zusammenhang ist die quantitative Analyse (Volumen der einzelnen Teilabschnitte) von Bedeutung. Die mikrobielle Symbiose, und damit die Möglichkeit zur alloenzymatischen Verdauung, ist ein wesentliches Kennzeichen der Säugetiere mit multilokulärem Magen. Sie ist in mehreren Stammeslinien unabhängig voneinander entstanden und ist von hohem Selektionswert als Anpassung an die Nutzung und Verwertung zellulosereicher Pflanzennahrung. Bei der vergleichenden Auswertung wird jener Anpassungstyp, bei dem die alloenzymatische Zerlegung im Colon lokalisiert ist (Perissodactyla) eingehend herangezogen. Die Arbeit bringt eine überzeugende Deutung in funktioneller und biologischer Hinsicht für die Unterschiede beider Adaptationstypen.

Das Buch ist gut, zum Teil spannend, zu lesen. Die 245 hervorragenden und originellen Abbildungen sind besonders hervorzuheben. Das vollständige Schriftenverzeichnis (47 S.) ist von großem Nutzen. Die Monographie von LANGER dürfte als Standardwerk für alle Morphologen, Ernährungswissenschaftler, Ökologen, Evolutionsbiologen und Veterinärwissenschaftler unentbehrlich sein. Zudem sei es als Pflichtlektüre für jene empfohlen, die meinen, Morphologie habe nichts wesentlich Neues zu bieten und sei eine überholte Disziplin.

D. STARCK, Frankfurt/M.

MACK, R.: **Dictionary for Veterinary Science and Biosciences.** German-English/English-German; with trilingual Appendix: Latin terms = Wörterbuch für Veterinärmedizin und Biowissenschaften. Berlin und Hamburg: Paul Parey 1988. 321 S. DM 49,80. ISBN 3-489-50516-6

Dieses Spezialwörterbuch hat gefehlt: es ergänzt die allgemeinen Wörterbücher in sinnvoller und vielfältiger Weise mit Termini technici aus den Gebieten der Anatomie, Physiologie, Mikrobiologie, Parasitologie, Pathologie, Pharmakologie, Toxikologie und Tierzucht. Schwerpunktmäßig stehen dabei Haustiere und ihre Erkrankungen im Vordergrund, weiter finden europäische Wildtiere und Zootiere Berücksichtigung. Die Gliederung erfolgt klassisch: einem Deutsch-Englisch-Abschnitt folgt die Übersetzung englischer Termini in deutsche; ein dritter Block ist dreisprachig: lateinische Begriffe (Anatomie – nach den „Nomina Antatomica Veterinaria" [NAV] – und Medizin) werden ins Deutsche wie ins Englische übertragen. Lateinische Namen aus dem Tier- und Pflanzenreich (europäische Wildtiere, Zootiere, Parasiten; Futter-, Gift- und Arzneimittelpflanzen) sind in den dreisprachigen Appendix eingereiht.

Studierenden der Tiermedizin und der biologischen Wissenschaften ist dieses Wörterbuch ebenso zu empfehlen wie Praktikern und Wissenschaftlern, Übersetzern, Bibliotheken und Behörden.

DORIT FEDDERSEN-PETERSEN, Kiel

GÖRNER, M.; HACKETHAL, H.: **Säugetiere Europas; beobachten und bestimmen.** Stuttgart: Ferdinand Enke 1988. 271 pp., 656 Abb., davon 225 farbig, DM 29,80, ISBN 3-432-96461-7

Das vorliegende Taschenbuch, das „über die Vielfalt der wildlebenden Tiere Europas informieren, zu Beobachtungen und zur Beschäftigung mit dieser Tiergruppe anregen will und eine zuverlässige Bestimmung der Arten ermöglichen" soll, darf als eine wichtige Neuerscheinung angesehen werden, wenngleich zu diesem Thema bereits mehrere deutschsprachige Taschenbücher vorliegen (V. D. BRINK; CORBET/OVENDEN; SCHILLING/SINGER/DILLER; DOBRORUKA/BERGER). Dem eigentlichen über 300 Seiten umfassenden Bestimmungsteil mit den Artbeschreibungen sind kürzere, einführende Kapitel vorangestellt: Kennzeichen der Säugetiere, Hinweise zur Benutzung des Buches einschließlich einiger Angaben über das Vermessen von Tieren und Schädeln, die Säugetierfauna Europas aus tiergeographischer Sicht, Säugetierschutz und Beobachtung von Säugetieren, wobei auch indirekte Methoden erwähnt werden (Fährten, Gewöllinhalte).

Aus der systematischen Übersicht geht hervor, daß 209 Arten vorgestellt werden, unter ihnen auch die gelegentlich strandenden Wale. Das vorliegende Buch enthält zahlreiche Bestimmungsschlüssel. Zwar gibt es keine Schlüssel zum Bestimmen der Säugetierordnungen, innerhalb der Ordnung finden sich aber Schlüssel, die für die Familien- und Gattungsbestimmung bis zur Bestimmung der einzelnen Arten nach äußeren und Schädelmerkmalen führen. Die meisten der erwähnten Arten sind in durchweg ansprechenden Farbzeichnungen dargestellt. Wichtige Bestimmungshilfen sind ferner Schwarz-Weiß-Zeichnungen, die über besondere Körper- und Schädelmerkmale, vor allem aber über Zahngröße, Zahnform, das Kauflächenbild der Zähne und die Wurzelzahl informieren.

Die Beschreibung der einzelnen Arten folgt weitgehend einem einheitlichen Schema: Kennzeichen mit Maßangaben, Vorkommen und Lebensweise mit oft ausführlichen, den neuesten Forschungsstand berücksichtigenden Anfagen über Lebensraum, Fortpflanzung, Jugendentwicklung und Ernährung. Jeder Art ist eine Verbreitungskarte beigegeben. Worterklärungen, eine Auswahl aus der weiterführenden Spezialliteratur und ein Register beschließen das rundum gelungene Taschenbuch, das bald zu den bekanntesten Büchern dieser Art gehören wird.

H. REICHSTEIN, Kiel

Subscription information for USA, Canada and Mexiko obtainable from Paul Parey Scientific Publishers/IR Unltd., 35 West 38th Street, Suite 3 W, New York, NY 10018, USA.

Erscheinungsweise und Bezugspreis 1989: 6 Hefte bilden einen Band. Jahresabonnement Inland: 318,– DM zuzüglich 13,80 DM Versandkosten, Gesamtpreis 331,80 DM einschließlich 7 % Mehrwertsteuer. Jahresabonnement Ausland: 318,– DM zuzüglich 18,– DM Versandkosten. Das Abonnement wird zum Jahresanfang berechnet und zur Zahlung fällig. Es verlängert sich stillschweigend, wenn nicht spätestens am 15. November eine Abbestellung im Verlag vorliegt. Die Zeitschrift kann bei jeder Buchhandlung oder bei der Verlagsbuchhandlung Paul Parey, Spitalerstraße 12, D-2000 Hamburg 1, bestellt werden. Die Mitglieder der „Deutschen Gesellschaft für Säugetierkunde" erhalten die Zeitschrift unberechnet im Rahmen des Mitgliedsbeitrages.

Z. Säugetierkunde 54 (1989) 3, 129–192

…), 193–264, August 1989 ISSN 0044-3468 C 21274 F

ZEITSCHRIFT FÜR SÄUGETIERKUNDE

INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde

Verlag Paul Parey Hamburg und Berlin

This journal is covered by Biosciences Information Service of Biological Abstracts, and by Current Contents (Series Agriculture, Biology, and Environmental Sciences) of Institute for Scientific Information

---

Die Zeitschrift für Säugetierkunde veröffentlicht Originalarbeiten und wissenschaftliche Kurzmitteilungen aus dem Gesamtgebiet der Säugetierkunde, Besprechungen der wichtigsten internationalen Literatur sowie die Bekanntmachungen der Deutschen Gesellschaft für Säugetierkunde. Verantwortlicher Schriftleiter im Sinne des Hamburgischen Pressegesetzes ist Prof. Dr. Harald Schliemann.

Zusätzlich erscheint einmal im Jahr ein Heft mit den Abstracts der Vorträge, die auf der jeweiligen Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde gehalten werden. Sie werden als Supplement dem betreffenden Jahrgang der Zeitschrift zugeordnet. Verantwortlich für ihren Inhalt sind ausschließlich die Autoren der Abstracts.

Manuskripte: Manuskriptsendungen sind zu richten an die Schriftleitung, z. Hd. Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Biologie-Zentrum, Neue Universität, Olshausenstr. 40–60, D-2300 Kiel. Für die Publikation vorgesehene Manuskripte sollen gemäß den „Redaktionellen Richtlinien" abgefaßt werden. In ihnen finden sich weitere Hinweise zur Annahme von Manuskripten, Bedingungen für die Veröffentlichung und die Drucklegung, ferner Richtlinien für die Abfassung eines Abstracts und eine Korrekturzeichentabelle. Die Richtlinien sind auf Anfrage bei der Schriftleitung und dem Verlag erhältlich.

Sonderdrucke: Anstelle einer Unkostenvergütung erhalten die Verfasser von Originalbeiträgen und Wissenschaftlichen Kurzmitteilungen 50 unberechnete Sonderdrucke. Mehrbedarf steht gegen Berechnung zur Verfügung, jedoch muß die Bestellung spätestens mit der Rücksendung der Korrekturfahnen erfolgen.

Mit drei Beilagen des Verlages Paul Parey

Fortsetzung 3. Umschlagseite

© 1989 Paul Parey. Verlag: Paul Parey, Hamburg und Berlin. Anschriften: Spitalerstr. 12, D-2000 Hamburg 1; Lindenstr. 44–47, D-1000 Berlin 61. – Printed in Germany by Westholsteinische Verlagsdruckerei Boyens & Co., D-2240 Heide/Holst.

Z. Säugetierkunde 54 (1989) 193–204
© 1989 Verlag Paul Parey, Hamburg und Berlin
ISSN 0044-3468

Developmental evidence for dental homologies in the monotreme *Ornithorhynchus* and its systematic implications

By W. P. LUCKETT and U. ZELLER

Abteilung Morphologie, Zentrum Anatomie der Universität Göttingen

Receipt of Ms. 27. 1. 1988

Abstract

Investigated the early development of the anterior cheek teeth in the platypus, *Ornithorhynchus anatinus* (order Monotremata), in order to assess its suggested similarities with the dental replacement pattern in marsupials. Histological serial sections of the head were examined for 12 ontogenetic stages, ranging from 8–10 mm embryos in incubated eggs to nestling, subadult, and adult animals. Results indicate that the small, abnormally developed, anterior cheek teeth ("dv") in both jaws do not develop successor teeth, contrary to previous reports. We conclude that the developmental pattern of the platypus dentition is completely different from that of marsupials, and that there is no evidence from dental ontogeny to support the union of monotremes and marsupials in a higher taxon Marsupionta, contrary to an earlier suggestion by KÜHNE (1973, 1977).

Introduction

The discovery of fossil dental and skeletal remains of the monotreme family Ornithorhynchidae in middle Miocene deposits of Australia (WOODBURNE and TEDFORD 1975; ARCHER et al. 1978; LESTER and ARCHER 1986) has renewed interest in the question of the phylogenetic relationships of extant monotremes to other mammals. Partly because of the retention of numerous primitive mammalian and reptile-like features in their skeleton and soft anatomy, the extant monotremes *Ornithorhynchus, Tachyglossus* and *Zaglossus* have long been separated from other extant mammals as the subclass Prototheria (GILL 1872; GREGORY 1910; SIMPSON 1945; HOPSON 1970; MCKENNA 1975). In addition, most students of fossil and living mammals have also acknowledged a close relationship between Metatheria (marsupials) and Eutheria (placentals) and unite them in the subclass Theria.

A notable exception to this hypothesis of a prototherian-therian dichotomy was the proposal by GREGORY (1947) that monotremes were derived from early Australasian marsupials, and that Monotremata and Marsupialia therefore should be classified together in a new subclass Marsupionta. Among the shared cranioskeletal, reproductive and soft anatomical features cited by GREGORY to support this hypothesis was the presence of only a single deciduous premolar in each jaw of the platypus *Ornithorhynchus* and in marsupials. "There is evidence of one milk tooth in each jaw, this being in the premolar region and recalling the conditions in marsupials" (GREGORY 1947, p. 16). Further corroboration for GREGORY's (1947) marsupiontan hypothesis was provided by KÜHNE (1973, 1977, 1987) in his cladistic analysis of dental replacement patterns in the platypus and other extant mammals. He claimed that marsupials and *Ornithorhynchus* are synapomorphic in exhibiting replacement at only a single postcanine tooth position, followed by four molars, in contrast to the plesiomorphic eutherian pattern of replacing three or four premolars.

KÜHNE's (1973, 1977) arguments were founded on his reinterpretation of the histological study by GREEN (1937) on tooth development in a series of platypus nestlings. GREEN (1937) reported that a small abnormal deciduous premolar ("dv") occurs in both jaws in specimens of 56–170 mm dorsal contour length (DCL). In addition, he claimed that in the lower jaw there was an "aborted tooth rudiment" for a successor of "dv" in some

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5404-0193 $ 02.50/0

specimens between 122–250 mm DCL. None of these rudimentary successor teeth was illustrated photographically, although GREEN (1937) included them in his schematic diagram of the idealized dentition of *Ornithorhynchus*. This diagram was reproduced by KÜHNE (1973, 1977) as evidence of tooth replacement for a single deciduous premolar in the platypus.

The marsupiontan hypothesis of GREGORY (1947) and KÜHNE (1973) has not been supported by comparative or cladistic analyses of numerous developmental, reproductive and cranioskeletal features in the three major groups of mammals (KUHN 1971; LUCKETT 1977; STARCK 1978; MARSHALL 1979; KUHN and ZELLER 1987; ZELLER 1987); instead, these analyses have provided strong corroboration for the traditional view of prototherian-therian dichotomy during mammalian phylogeny. Although several authors (PARRINGTON 1974; GRIFFITHS 1978; STARCK 1978; THENIUS 1979; MARSHALL 1979; AX 1984) have questioned KÜHNE's interpretation of tooth homologies in *Ornithorhynchus*, none has falsified his hypothesis by directly examining aspects of dental development in the platypus.

Recently, we have investigated various aspects of cranial (KUHN and ZELLER 1987; ZELLER 1987, in press, in prep.) and dental development (LUCKETT and ZELLER in prep.) in an extensive series of embryonic and nestling *Ornithorhynchus anatinus*, in order to clarify aspects of cranial and dental homologies and character state polarities among the major mammalian subgroups. In the present study, we limit ourselves to observations that relate to the suggested identification of a single deciduous and successor premolar in each jaw of the platypus, and to the systematic conclusions that KÜHNE (1973, 1977) has drawn from his postulated tooth homologies in this animal. We shall try to answer three interrelated questions in our ontogenetic analysis.

1. What is the evidence for identifying four molars and a single premolar in each jaw quadrant of *Ornithorhynchus?*
2. Is there distinct evidence for tooth replacement of a deciduous premolar?
3. Is the pattern of dental homologies and replacement synapomorphous for *Ornithorhynchus* and marsupials?

Material and methods

The 12 ontogenetic stages examined during this study ranged from 8–10 mm GL embryos in unhatched eggs to a series of nestling, subadult and adult stages (Table 1). Eight specimens were obtained from the collection of the late Professor J. P. HILL; this collection is currently maintained at the Hubrecht Laboratory, Utrecht, the Netherlands. Additional specimens were acquired from the American Museum of Natural History, New York, New York; National Museum of Natural

Table 1. **Ontogenetic stages of *Ornithorhynchus anatinus* studied**

Specimen	Specimen Number	Stain
8 mm GL Embryo	M 37 (Hub. Lab.)	H & E
9 mm GL Embryo	M 38 (Hub. Lab.)	H & E
9 mm GL Embryo*	MO 7 (Hub. Lab.)	Alcianblue
10 mm GL Embryo	M 42 (Hub. Lab.)	H & E
16.75 mm GL Newly-hatched (28 mm DCL)	M 44 (Hub. Lab.)	H & E
56 mm DCL Nestling	M 45 (Hub. Lab.)	H & E
74 mm DCL Nestling*	AMNH 201969	Azan
122 mm DCL Nestling*	MO 38 (Hub. Lab.)	Azan
180 mm DCL Nestling*	MO 39 (Hub. Lab.)	Azan
333 mm DCL Nestling*	USNM 221112	Azan
55.5 mm HL Nestling*	AMNH 201312	Azan
400 mm Total length Adult*	Coll. Dr. W. Hecker	Azan; H & E

History, Washington, D. C.; and from the Collection of Dr. W. HECKER, München. The heads of five of the embryonic and early nestling stages were sectioned previously, and some of these were studied by GREEN (1937). The preserved heads of the remaining seven specimens, marked by an asterisk in Table 1, were embedded in paraffin or celloidin and sectioned serially at 10–80 μm at the Abteilung Morphologie of the Zentrum Anatomie, Universität Göttingen (KUHN and ZELLER 1987; ZELLER 1987, in press, in prep.). Sections were stained with either Hematoxylin and Eosin (H and E) or Azan. Because of the unusual shape of the head and tail of posthatching *Ornithorhynchus*, we have adopted the "dorsal contour line" (DCL) measurement of WILSON and HILL (1907) and GREEN (1937) for our specimens. This measurement is taken along the dorsal curvature of the body, from the tip of the snout to the tip of the tail. Measurements of the embryonic and newly-hatched specimens in the HILL collection are documented according to their greatest length (GL). Serial sections were examined for each jaw quadrant, in order to record the developmental state of all tooth germs or thickenings of the dental lamina.

Results

Disagreement exists concerning the premolar or molar homologies of some of the transitory cheek teeth in *Ornithorhynchus;* therefore, we follow WILSON and HILL (1907) and GREEN (1937) in adopting the designation "dv", "w", "x", "y" and "z" for the five cheek teeth that appear mesiodistally during posthatching life in each jaw quadrant of the platypus. The ontogeny of each of these teeth will be described in detail elsewhere (LUCKETT and ZELLER in prep.). In the present study we focus only on the development of the most anterior (= mesial) of these cheek teeth.

The bilateral dental laminae are evident as thickenings of the oral epithelium in the upper jaws of 8–9 mm platypus embryos, before the onset of ossification in the future praemaxillary, maxillary or dentary bones. Dental laminae are also present, although less differentiated, in the lower jaw. In the 10 mm embryo, there is a distinct bud-like thickening of the dental lamina at the level of the rostral extent of the early maxillary ossification, and a more elongate bud-like thickening of the lamina lies at the distal extent of the Os maxillare (Table 2). This latter bud-like swelling is overlain by the distal half of the developing eye. The lower lamina also exhibits two comparable thickenings, although the distal swelling is shallower, but wider, than that of the upper lamina.

In a newly-hatched platypus (16.75 mm GL; 28 mm DCL), prominent swellings also occur near the distal end of the dental lamina in both jaws. The elongate bud of the upper jaw is present just in front of the anterior margin of the small eye. The comparable thickening in the lower jaw is wider buccolingually, and it is asymmetrically indented on its inferior surface by the underlying mesenchyme to form an early cap stage (Fig. 1). The epithelium of this tooth germ is in broad communication with the overlying oral epithelium, so that an elongate dental lamina strand is not evident between the two epithelia. By comparison with later stages, as well as by observing its relationships to the developing eye and other cranial landmarks, this developing tooth germ is homologous with "dv" of later stages in both jaws, and to the distal bud-like swellings of the dental laminae in the 10 mm embryo. In this newly-hatched stage, the dental lamina extends slightly distal to "dv" in both jaws, but it does not yet form a distinct bud distal to this tooth germ.

In the next available stage, a nestling of 56 mm DCL, "dv" is considerably advanced developmentally in both jaws. Upper "dv" is in the bell stage and has a thin layer of dentin differentiated over its apex (Fig. 2). This small tooth is clearly abnormal in several respects. It remains in broad continuity with the oral epithelium and projects only slightly into the underlying mesenchyme. The inner enamel epithelium adjacent to the thin dentinal cap is overlain by a zone of slightly loosened epithelial cells, but the latter does not form a distinct stratum of stellate reticulum, nor is the outer enamel epithelial layer of the tooth germ clearly delimited from the overlying oral epithelium (Fig. 2). The comparable tooth in the lower jaw is less mature, and shows only a very thin layer of early predentin.

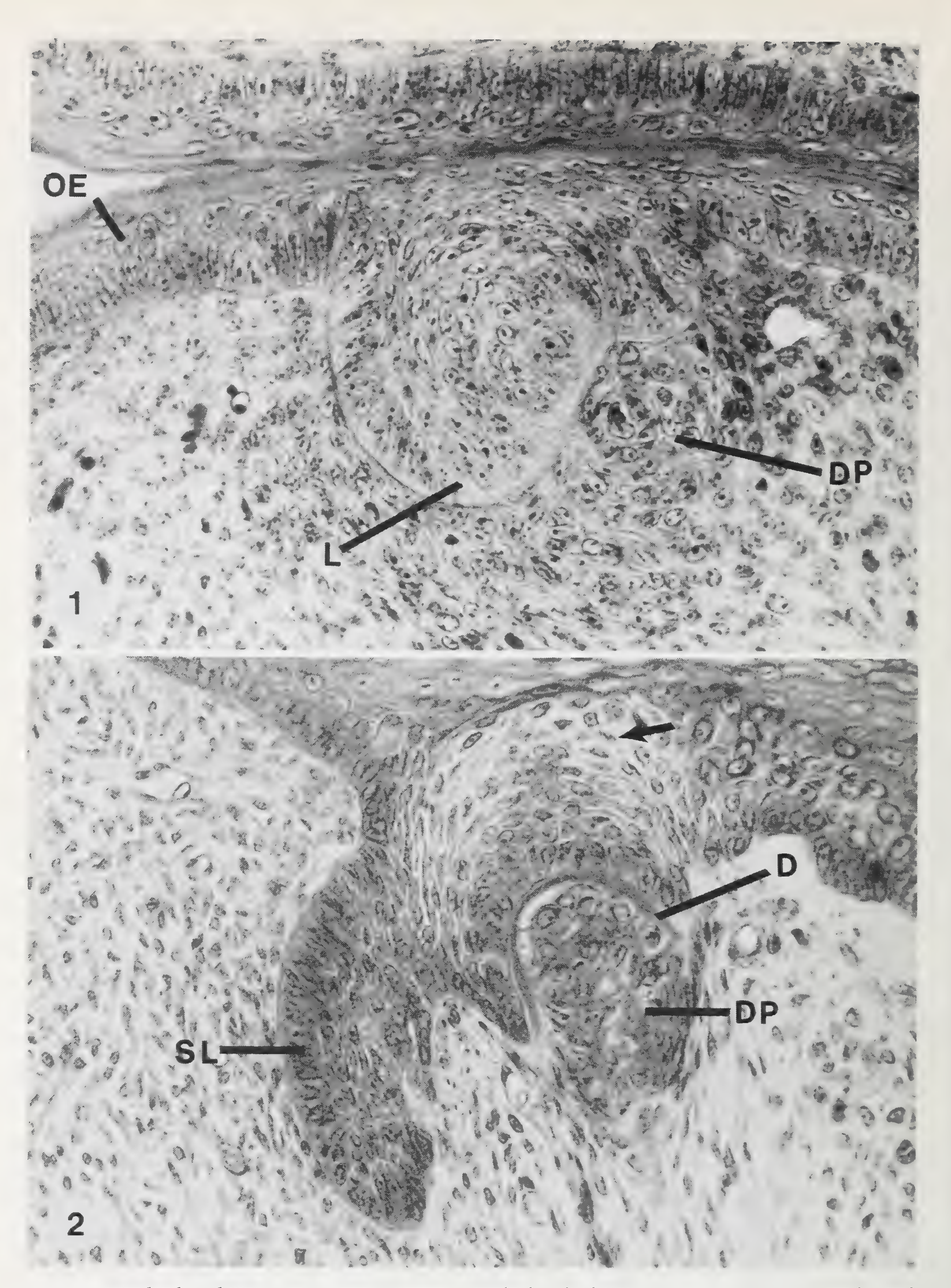


Fig. 1. Ornithorhynchus anatinus 28 mm DCL newly-hatched young. Transverse section through lower jaw at the level of the thickened early cap stage for "dv". Note the broad attachment of the tooth germ to the overlying oral epithelium (OE), and the asymmetry of the cap stage, with a smaller, darkly-stained buccal portion (at right), and a larger, inferiorly-projecting lingual portion (L). Early mesenchymal condensation is evident in the developing dental papilla (DP). (× 400)

Fig. 2. Ornithorhynchus anatinus 56 mm DCL nestling. Transverse section through bell stage upper "dv", showing broad attachment to the oral epithelium, and early dentin (or predentin) cap (D) overlying the dental papilla (DP). Note the slight loosening of cells (arrow) marking the site of the potential stellate reticulum, and the slightly curved lingual „successional" lamina (SL), continuous with the oral epithelium and the outer enamel epithelium of the abnormal "dv". (× 400)

A ridge-like successional lamina lies at the lingual side of the abnormal "dv", and it projects deeper into the jaw stroma than does the buccal "dv". The lingual successional lamina is continuous with the poorly-defined outer enamel epithelium of "dv" and with the oral epithelium (Fig. 2). Although the successional lamina appears to be slightly swollen, it is comparable in thickness to, and continuous with, the primary dental lamina that extends mesial to "dv".

In contrast to the abnormal appearance of the small "dv" in the upper jaw, the larger tooth developing distal to this (tooth "w") appears to be a relatively normal late bell stage, with moderately developed stellate reticulum, no odontoblasts or dentin, and no evidence for a lingual "successional" lamina (see Table 2). This tooth has undergone considerable development since the 28 mm DCL newly-hatched stage, where is was represented only by a short extent of the dental lamina. A similar tooth "w" also occurs in the lower jaw of the 56 mm DCL nestling.

In a later nestling of 74 mm DCL, "dv" is represented in both jaws by a relatively small, abnormal, irregular dentinal knot, in which scattered stromal cells and odontoblasts are entrapped (Fig. 3). As in the previous stage, the inner enamel epithelium is adherent to the basal surface of the oral epithelium, and a loosening of cells within the adjacent oral epithelium represents an abortive attempt at formation of stellate reticulum. The inner enamel epithelium does not differentiate into ameloblasts, and there is no formation of enamel in the abnormal "dv" of this or later stages. The lingual successional lamina ridge retains the same relative size and relationships as in the previous stage, in contrast to the further differentiation of the abnormal dentinal knot. The successional lamina is continuous distally with the primary dental lamina between "dv" and "w".

The tiny, abnormal dentinal knot of "dv" has become more detached or delimited from the oral epithelium of both jaws in a 122 mm DCL nestling, and its lingual successional lamina is now relatively thin and folded, and it shows early evidence of fragmentation

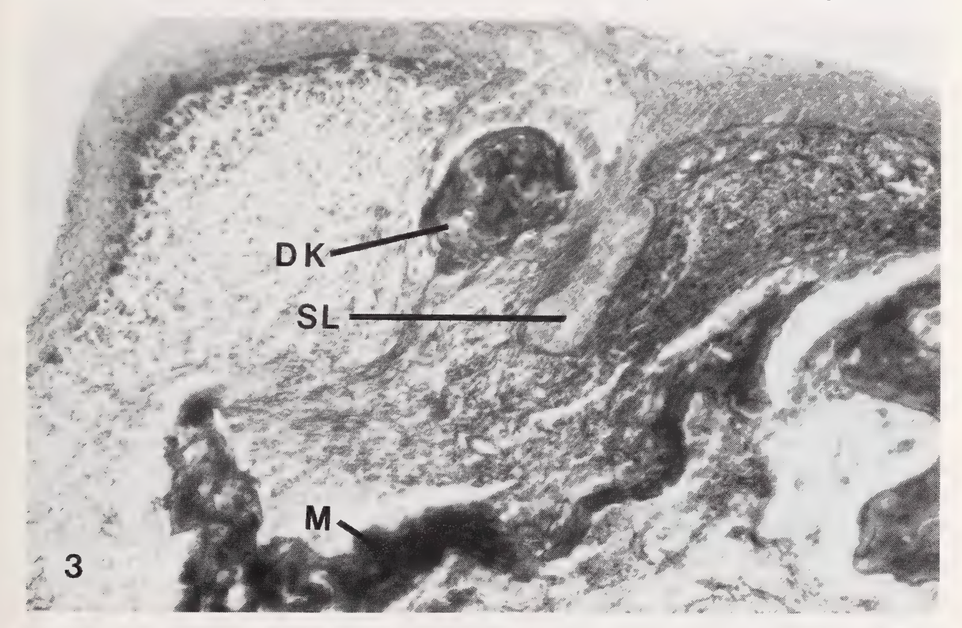


Fig. 3. Ornithorhynchus anatinus 74 mm DCL nestling. Transverse section through upper jaw with "dv" represented by an irregular dentinal knot (DK), closely adherent to the adjacent oral epithelium. The lingual "successional" lamina (SL) has not increased in thickness since the previous stage. Note the underlying maxillary bone trabeculae (M), partly detached from the adjacent mesenchyme. (× 256)

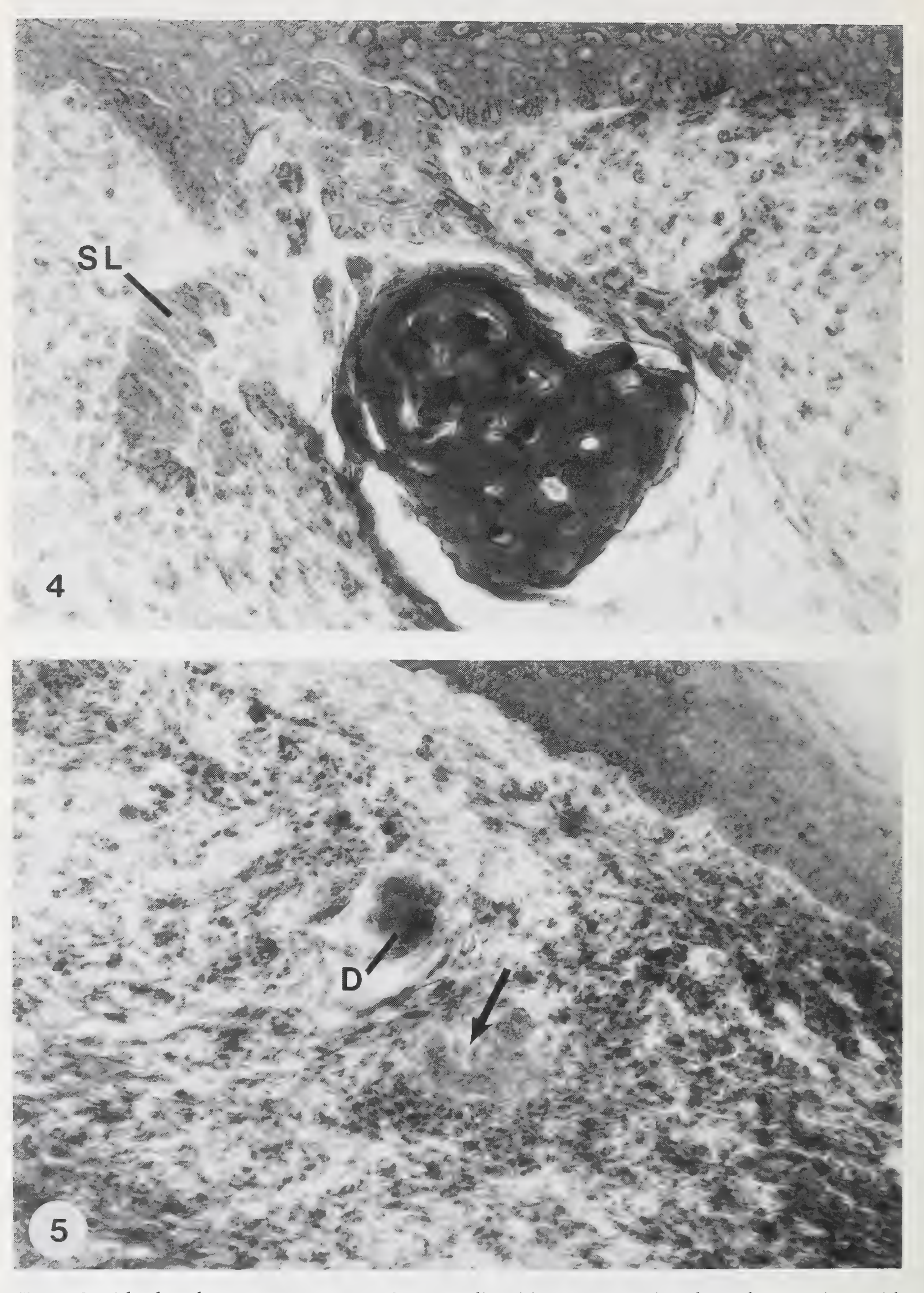


Fig. 4. Ornithorhynchus anatinus 122 mm DCL nestling. Transverse section through upper jaw, with irregular dentinal knot of “dv” beginning to become detached from the oral epithelium. Note the folded and early fragmented nature of the lingual “successional” lamina (SL). (× 400)

Fig. 5. Ornithorhynchus anatinus 180 mm DCL nestling. Transverse section through lower jaw, with tiny dentinal fragment (D) representing the last remnant of abnormal “dv”. An isolated, folded remnant of the lingual “successional” lamina is still evident (arrow). (× 256)

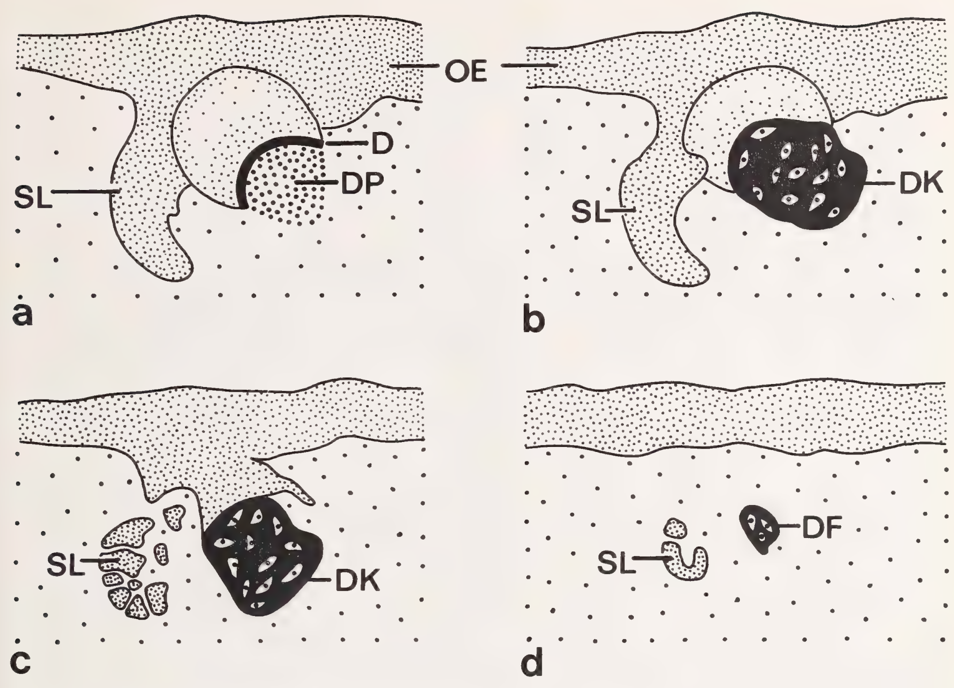


Fig. 6. Diagram of the ontogenetic relationships between the oral epithelium (OE), abnormal tooth "dv", and its successional lamina (SL) in *Ornithorhynchus anatinus* nestlings. Upper jaw of: a = 56 mm DCL; b = 74 mm DCL; c = 122 mm DCL nestlings. d = Lower jaw of 180 mm DCL nestling, with tiny, isolated dentinal remnant (DF) of "dv", as well as fragmented lingual successional lamina. D = Dentinal arc; DK = Dentinal knot; DP = Dental papilla

(Fig. 4), especially in the lower jaw. In the next available stage, a 180 mm DCL nestling, there is no trace of "dv" in the upper jaw, although a tiny isolated strand of dental lamina lying free within the stroma at the appropriate position may represent the last remnant of the successional lamina for "dv". In the lower jaw, a minute, irregular dentinal fragment lies free beneath the oral epithelium, and lingual to it is an isolated piece of flattened dental lamina (Fig. 5). These doubtlessly represent the last vestiges of "dv" and its successional lamina. No remnant of "dv" or its successor lamina was detected in a more mature 333 mm DCL nestling. A comparison of selected stages in the development and regression of "dv" is presented in Figure 6, and the major structural features of this tooth during ontogeny are compared to those of the more normal tooth "w" in Table 2.

Discussion

The observations of the present study provide no evidence to support the hypothesis that there is a rudimentary successor tooth for the small, abnormal deciduous premolar ("dv") of *Ornithorhynchus*. The earliest suggestion for "replacement" of a deciduous cheek tooth in the platypus was presented by WILSON and HILL (1907), based on their study of two juveniles. They described and illustrated a small, calcified deciduous tooth ("dv") with a slightly swollen lingual successional lamina, in both jaws of an 80 mm DCL nestling. In an older 250 mm stage, they found no trace of the abnormal "dv". However, they described "a small and rudimentary, but distinctly papillated, enamel-organ" (WILSON and HILL

Table 2. **Developmental stages of "dv" and "w" in the upper jaw of *Ornithorhynchus***

Specimen	"dv"	Successor lamina of dv	"w"
10 mm GL Embryo	Distinct early bud-like thickening	–	–
16.75 mm GL (28 mm DCL) Newly-hatched	Distinct bud-like swelling	–	Dental lamina
56 mm DCL Nestling	Tiny, abnormal tooth; thin dentinal arc	Slightly swollen	Moderately large, late bell, no odontoblasts
74 mm DCL Nestling	Tiny, abnormal, irregular dentinal knot	Slightly swollen	Moderately large, late bell, early dentin; no distinct residual lamina
122 mm DCL Nestling	Tiny, abnormal, irregular dentinal knot	Flattened; early fragmentation	Large, late bell, moderately thick dentin; short residual lamina
180 mm DCL Nestling	No trace	Tiny dental lamina fragment	Moderate sized, thick dentin, thin enamel; irregular residual lamina
333 mm DCL Nestling	No trace	No trace	Moderate sized, thick dentin, moderately developed enamel; no distinct residual lamina

1907, p. 145) in the appropriate position in the upper jaw, and they considered this to be evidence of a true successor (tooth "v") for the missing "dv".

Wilson and Hill (1907, p. 148) suggested that the slightly enlarged lingual lamina of the younger stage was the "genuine representative" of the small "imperfectly formed" tooth "v" that they identified in the later 250 mm specimen. If this were true, then it would be expected that the lingual successional lamina of "dv" would exhibit intermediate stages of enlargement and differentiation in the platypus nestlings between 80–250 mm DCL described by Green (1937) and by us during the present investigation.

The nature of the successional lamina for "dv" in the 122 mm and 140 mm DCL nestlings was not described or illustrated by Green (1937), although he claimed to find evidence of an "aborted tooth rudiment" for successor "v" immediately in front of the abnormal lower "dv" in his 122 mm stage. Apparently, he detected no trace of a successor tooth "v" in the 140 mm stage, although "dv" was still represented by an abnormal dentinal knot. Green (1937) did not describe "dv" or "v" in his 200, 225, 250, and 295 mm DCL nestlings. Unfortunately, no photographs of the socalled rudimentary "successor" teeth were provided by Wilson and Hill or by Green. Despite this lack of documentation, Green (1937, p. 394) presented an "anachronistic diagram to show the ideal dentition of *Ornithorhynchus*", in which he illustrated the presence of both a deciduous and "replacing" tooth at the "v" position in both jaws.

In contrast, our study indicates that there is no relative increase in thickness of the lingual successional lamina of "dv" in specimens of 56, 74, 122, and 180 mm DCL, nor does this lamina differentiate into a distinct bud or cap stage. Indeed, the successional lamina of the 122 mm nestling is less differentiated than in the younger specimens, as evidenced by its relative thinness and early fragmentation; this is followed by greater fragmentation and loss of the successional lamina in the 180 mm nestling. It is possible that Green (1937) misinterpreted the folded and fragmented lingual lamina in his 122 mm DCL specimen as a distinct tooth rudiment for a successor "v". He also illustrated (Green 1937,

Fig. 42), but did not describe, a flattened and fragmented lingual successional lamina adjacent to a small dentinal knot remnant for "dv" in the lower jaw of a 170 mm DCL nestling, similar to the condition in our 180 mm specimen.

Teeth "dv" and "w" were considered to be premolars by WILSON and HILL (1907) and GREEN (1937), based in part on their small size and minimal degree of cusp differentiation, whereas the larger, multicuspidate, more distal teeth "x", "y", and "z" were identified as molars. However, tooth "w" was reinterpreted as a molar by KÜHNE (1973, 1977), because it shows no evidence of replacement. He emphasized that presence of absence of replacement, rather than size or shape, should be the main criterion for identifying premolars or molars. Although there is no evidence for development of a successor for tooth "dv", the pattern of early differentiation of the dentition in *Ornithorhynchus* is consistent with, but by no means proves, the hypothesis that this is a deciduous premolar, which is unreplaced during ontogeny. Comparison of the development of the dental lamina and early tooth buds with the state of differentiation of the nasal septum, Meckel's cartilage, jaw ossifications, and the eye in 8–10 mm platypus embryos with similar ontogenetic stages in marsupials and eutherians (LUCKETT 1988) suggests that the pattern of early dental development is homologous in the three major mammalian groups. Moreover, the two early tooth buds in the platypus upper jaw differentiate in association with the rostral and caudal extents of the early maxillary ossification, indentical with the developmental pattern for the deciduous canine and a posterior deciduous premolar (dP3 or dP4) in therians. Further development of the deciduous canine in the platypus is even more abnormal and more transitory than that of "dv" (GREEN 1937; LUCKETT and ZELLER in prep.).

HILL and DE BEER (1950) claimed that tooth "dv" is not serially homologous with mammalian deciduous teeth, because they believed that the former is not derived from the primary dental lamina, but instead differentiates directly from the oral epithelium that lies buccal to the dental lamina. However, our observations on earlier developmental stages clearly indicate that "dv" is derived from an early bud of the dental lamina, and that only secondarily does the abnormal tooth become displaced buccally. In later stages, "dv" in the platypus forms an abnormal dentinal knot, fails to develop enamel or a successor tooth, and is resorbed without erupting. This pattern of abnormal development and resorption of a deciduous premolar in *Ornithorhynchus* is convergently similar to the conditions for the abnormal first deciduous incisor in rodents and lagomorphs (LUCKETT 1985).

We agree with SIMPSON (1929) that it is difficult to resolve the premolar-molar homology of tooth "w" at present, due to the varying degree of abnormality for the entire dentition in the platypus. Tooth "w" is initiated somewhat later in ontogeny than is "dv", but the developmental gap between our 28 and 56 mm DCL nestlings makes it more difficult to assess the deciduous premolar or molar homologies of tooth "w" using embryological criteria. The possible indentification of this tooth as a molar is provided by the nature of the epithelial lamina that differentiates at the lingual side of tooth "w". This lingual lamina is a poorly developed and transitory structure (Table 2) and is most comparable to the "residual lamina" of therian molars and successional antemolars, rather than to a "successional lamina". Such a residual lamina is not known to give rise to tooth germs in any extant mammal. Even though tooth "w" is more normal during its ontogeny than the small, abnormal "dv", its lingual lamina is more slender and less differentiated than that of "dv". These observation would be consistent with a hypothesis that the unreplaced tooth "w" is a molar rather than a premolar.

Nevertheless, the small size and nonmolariform nature of tooth "w" suggest that it is an unreplaced posterior deciduous premolar, rather than a molar. The known pattern of molar reduction and loss in mammals also supports this hypothesis. In fossil and extant mammals that have lost molars during phylogeny, such as some carnivores, macroscelidids, muroid rodents, and platyrrhine primates, comparative and ontogenetic studies indicate that molars are lost at the distal rather than the mesial end of the tooth row (LECHE

1895; Ziegler 1971). The reduced size of the last lower molar (tooth "z") in *Ornithorhynchus*, coupled with its virtual loss in the upper jaw (Green 1937; Luckett and Zeller, in prep.), is also consistent with these observations. We acknowledge, however, that our interpretation of premolar-molar homologies in *Ornithorhynchus* must remain tentative, due to the reduction and varying degree of abnormality of the entire dentition in the platypus, as well as to the complete lack of tooth germs, with the exception of the so-called egg tooth, in the echidna *Tachyglossus* (Seydel 1899).

Finally, the present investigation provides no evidence to support Kühne's (1973, 1977) hypothesis of monotreme-marsupial affinities, based on the supposed synapomorphy of homologous patterns of postcanine dental replacement. Our disagreement with Kühne occurs at two different levels. First, our ontogenetic study demonstrates the lack of differentiation of a distinct tooth germ on the lingual "successional" lamina of "dv", even though the supposed presence of a successor tooth at this locus was the central argument for Kühne's support of the marsupiontan hypothesis. As far as we can determine, Kühne examined no developmental stages of *Ornithorhynchus*, but relied instead on Green's (1937) poorly documented (and ultimately erroneous) report for the presence of such a successor tooth.

Secondly, we believe that the entire premise of Kühne's (1973, 1977) systematic argument for Marsupionta is poorly founded. Even if we had detected evidence for a single deciduous and successional premolar locus in *Ornithorhynchus*, this would still not indicate a probable synapomorphy shared with marsupials. Other mammals, such as caviomorph rodents, have the promolars reduced to a single locus in each jaw, with replacement of the deciduous premolar occurring in most cases (Luckett 1985). However, if a successor tooth for "dv" did develop in *Ornithorhynchus*, this would not constitute a synapomorphy shared with caviomorphs. If only a single premolar locus is present (as suggested by Kühne for the platypus), then only a single premolar locus could be replaced. On the other hand, marsupials are unique (= autapomorphous) among mammals in replacing only the last of the three premolar loci that occur in each jaw quadrant (Kükenthal 1891).

Kühne (1973) appears to have been overly optimistic in his analysis of marsupiontan affinities when he claimed (p. 61) that "if only one synapomorphy is found and recognized as such, and generally acknowledged, the problem is solved". Hennig (1966) emphasized that there are no simple and absolutely dependable criteria for distinguishing among synapomorphy, convergence, or parallelism, and that hypotheses of synapomorphy must therefore be continually tested and rechecked. Although Kühne's single dental synapomorphy for Marsupionta has not been "generally acknowledged" or accepted by most systematists, we share his concern (Kühne 1987) that this suggested synapomorphy has been dismissed by them as convergence, without any real evidence, other than by an appeal to parsimony. As shown in the present study, developmental evidence for a successor premolar in *Ornithorhynchus* is lacking; therefore, we falsify Kühne's hypothesis that a dental replacement synapomorphy exists between monotremes and marsupials. In conclusion, no corroboration of a special phylogenetic relationship between monotremes and marsupials is provided by our study of dental development and homologies in *Ornithorhynchus*.

Acknowledgements

The authors acknowledge the use of material of the Embryological Collection of the Hubrecht Laboratory, Netherlands Institute for Developmental Biology, Utrecht, The Netherlands, viz., the following specimens: *Ornithorhynchus anatinus* M 37, M 38, MO 7, M 42, M 44, M 45, MO 38, and MO 39. We wish to thank Dr. G. Musser, American Museum of Natural History, New York, New York, Dr. R. W. Thorington, National Museum of Natural History, Washington, D.C., and Dr. A. Lechleuthner, München, for the loan of *Ornithorhynchus* specimens (see Table 1). The expertise of Mrs. Jutta Zeller in the preparation of the new serial sections is gratefully acknowledged. The

authors thank Dr. NANCY HONG and Frau JOHANNA KÜHN for their help with the photographic work, and Mr. EGBERT VON BISCHOFFSHAUSEN for the drawing. We are indebted to Prof. DR. HANS-JÜRG KUHN for critically reading the manuscript. This study was supported in part by the Deutsche Forschungsgemeinschaft (Project Ku 131/7–1), and by a Senior U.S. Scientist Award from the Alexander von Humboldt Foundation, Bonn, to W. P. LUCKETT.

Zusammenfassung

Zur Ontogenese der Zähne von Ornithorhynchus und ihre Bedeutung für die systematische Stellung der Monotremen

Nach GREGORY (1947) und KÜHNE (1973) stimmen das Schnabeltier, *Ornithorhynchus anatinus* (Ordnung: Monotremata) und die Beuteltiere (Marsupialia) darin überein, daß in der Ontogenese nur ein Zahn gewechselt wird. Aufgrund dieser Übereinstimmung sollen die Monotremen mit den Marsupialiern näher verwandt sein als mit den plazentalen Säugern (Eutheria); sie bilden nach GREGORY und KÜHNE gemeinsam das Taxon „Marsupionta". Die bisherigen Angaben über die Ontogenese der Zähne von *Ornithorhynchus* sind lückenhaft. Zur Klärung der Fragen nach Vorkommen oder Fehlen eines Zahnwechsels und möglicher Übereinstimmung mit den Verhältnissen bei den Beuteltieren wurde die Ontogenese der Zähne von *Ornithorhynchus* anhand von 12 Schnittserien durch Köpfe von Embryonen (8–10 mm GL), Nestjungen sowie von einem subadulten und einem adulten Tier untersucht. Das Frontzahngebiß von *Ornithorhynchus* ist stark reduziert. Im Gegensatz zu älteren Angaben entsteht an dem kleinen, stark reduzierten, fünftletzten Zahnkeim „dv", der bereits vor dem Durchbruch resorbiert wird, keine Ersatzzahnanlage. Die Zahnleiste lingual von „dv" entwickelt sich in der Ontogenese nicht weiter, sondern zerfällt in einzelne Fragmente und wird, ebenso wie „dv", restlos resorbiert. Auch keiner der nach distal folgenden Zähne „w", „x", „y" oder „z" wird gewechselt. Die Ontogenese der Zähne von *Ornithorhynchus* weist hinsichtlich des Zahnwechsels keinerlei Übereinstimmung mit derjenigen der Beuteltiere auf und gibt deshalb auch keine Hinweise auf eine nähere Verwandtschaft der Monotremen zu den Marsupialiern. Auf der Grundlage der Zahnentwicklung läßt sich das Taxon „Marsupionta" nicht begründen. Demgegenüber ist die systematische Einheit „Theria" (Marsupialia und Eutheria) aufgrund zahlreicher Synapomorphien von Beuteltieren und plazentalen Säugern sicher begründet.

References

ARCHER, M.; PLANE, M. D.; PLEDGE, N. S. (1978): Additional evidence for interpreting the Miocene *Obdurodon insignis* Woodburne and Tedford, 1975, to be a fossil platypus (Ornithorhynchidae: Monotremata) and a reconsideration of the status of *Ornithorhynchus agilis* De Vis, 1885. Aust. Zool. **20**, 9–27.

AX, P. (1984): Das phylogenetische System. Stuttgart, New York: G. Fischer.

GILL, T. (1872): Arrangement of the families of mammals and synoptical table of the characters of the subdivisions of mammals. Smithsonian Misc. Coll. **11**, 1–98.

GREEN, H. L. H. H. (1937): The development and morphology of the teeth of *Ornithorhynchus*. Phil. Trans. Roy. Soc. London, Series B **228**, 367–420.

GREGORY, W. K. (1910): The orders of mammals. Bull. Am. Mus. nat. Hist. **27**, 1–524.

— (1947): The monotremes and the palimpsest theory. Bull. Am. Mus. nat. Hist. **88**, 1–52.

GRIFFITHS, M. (1978): The biology of the monotremes. New York, San Francisco, London: Academic Press.

HENNIG, W. (1966): Phylogenetic systematics: Urbana: University of Illinois Press.

HILL, J. P.; DE BEER, G. R. (1950): Development of the Monotremata. Part VII. The development and structure of the egg-tooth and caruncle in marsupials. Trans. Zool. Soc. Lond. **26**, 503–544.

HOPSON, J. A. (1970): The classification of nontherian mammals. J. Mammalogy **51**, 1–9.

KÜHNE, W. G. (1973): The systematic position of monotremes reconsidered (Mammalia). Z. Morph. Tiere **75**, 59–64.

— (1977): On the Marsupionta, a reply to Dr. Parrington. J. nat. Hist. **11**, 225–228.

— (1987): Marsupionta contra Theria. In: Deutsche Ges. Säugetierkunde, 61. Hauptversammlg., Kurzfassungen der Vorträge u. Posterdemonstr. Ed. by C. Schmidt. Hamburg, Berlin: Paul Parey, 26–27.

KÜKENTHAL, W. (1891): Das Gebiß von *Didelphys*. Anat. Anz. **6**, 658–666.

KUHN, H.-J. (1971): Die Entwicklung und Morphologie des Schädels von *Tachyglossus aculeatus*. Abh. senckenb. naturforsch. Ges. **528**, 1–224.

KUHN, H.-J.; ZELLER, U. (1987): The Cavum epiptericum in monotremes and therian mammals. In: Morphogenesis of the mammalian skull. Ed. by H.-J. Kuhn and U. Zeller. Mammalia depicta, (Beihefte Z. Säugetierkunde) Nr. 13, 51–70.

Leche, W. (1895): Zur Entwicklungsgeschichte des Zahnsystems der Säugetiere. Theil I, Ontogenie. Bibliotheca Zoologica **17,** 1–160.
Lester, K. S.; Archer, M. (1986): A description of the molar enamel of a middle Miocene monotreme (*Obdurodon,* Ornithorhynchidae). Anat. Embryol. **174,** 145–151.
Luckett, W. P. (1977): Ontogeny of amniote fetal membranes and their application to phylogeny. In: Major patterns in vertebrate evolution. Ed. by M. K. Hecht, P. C. Goody and B. M. Hecht. New York: Plenum Press. pp. 439–516.
— (1985): Superordinal and intraordinal affinities of rodents: developmental evidence from the dentition and placentation. In: Evolutionary relationships among rodents. A multidisciplinary analysis. Ed. by W. P. Luckett and J.-L. Hartenberger. New York, London: Plenum Press. pp. 227–276.
— (1988): Early development and homology of the dental lamina and tooth buds in eutherian, metatherian, and prototherian mammals. Anat. Rec. **220,** 60A.
Luckett, W. P.; Zeller, U.: Development of the teeth in *Ornithorhynchus,* and its implications to the phylogeny of mammals. (In prep.)
Marshall, L. G. (1979): Evolution of metatherian and eutherian (mammalian) characters: a review based on cladistic methodology. Zool. J. Linn. Soc. **66,** 369–410.
Mckenna, M. C. (1975): Toward a phylogenetic classification of the Mammalia. In: Phylogeny of the primates. A multidisciplinary approach. Ed. by W. P. Luckett and F. S. Szalay, New York, London: Plenum Press. pp. 21–46.
Parrington, F. R. (1974): The problem of the origin of the monotremes. J. nat. Hist. **8,** 421–426.
Seydel, O. (1899): Über Entwickelungsvorgänge an der Nasenhöhle und am Mundhöhlendache von *Echidna* nebst Beiträgen zur Morphologie des peripheren Geruchsorgans und des Gaumens der Wirbeltiere. Semon. Zool. Forschungsreisen in Australien **3,** 2 (2), 445–532.
Simpson, G. G. (1929): The dentition of *Ornithorhynchus* as evidence of its affinities. Am. Mus. Novit. **390,** 1–15.
– (1945): The principles of classification and a classification of mammals. Bull. Am. Mus. nat. Hist. **85,** 1–350.
Starck, D. (1978): Das evolutive Plateau Säugetier. Sonderbd. naturwiss. Verein Hamburg **3,** 7–33.
Thenius, E. (1979): Die Evolution der Säugetiere. Stuttgart: G. Fischer.
Wilson, J. T.; Hill, J. P. (1907): Observations on tooth-development in *Ornithorhynchus*. Quart. J. Microscop. Sci. **51**, 137–165.
Woodburne, M. O.; Tedford, R. H. (1975): The first Tertiary monotreme from Australia. Am. Mus. Novit. **2588**, 1–11.
Zeller, U. (1987): Die Schädelentwicklung von *Ornithorhynchus* und die systematische Stellung der Monotremen. Deutsche Ges. Säugetierkunde, 61. Hauptversammlg., Kurzfassungen der Vorträge und Posterdemonstr. Ed. by C. Schmidt. Hamburg, Berlin: Paul Parey. pp. 55–56.
– (in press): The braincase of *Ornithorhynchus*. In: Fortschritte der Zoologie. Vol. **35**. Ed. by H. Splechtna, and H. Hilgers. Stuttgart, New York: G. Fischer.
– : Die Ontogenese und Morphologie des Schädels von *Ornithorhynchus anatinus* (In prep.)
Ziegler, A. C. (1971): A theory of the evolution of therian dental formulas and replacement patterns. Quart. Rev. Biol. **46,** 226–249.

Authors' addresses: Dr. W. Patrick Luckett, Department of Anatomy, University of Puerto Rico School of Medicine, GPO Box 5067, San Juan, Puerto Rico 00936, USA; and Dr. Ulrich Zeller, Abt. Morphologie, Zentrum Anatomie der Universität Göttingen, Kreuzbergring 36, D-3400 Göttingen, FRG

Z. Säugetierkunde 54 (1989) 205–214

ISSN 0044-3468

Medial tines on the upper incisors and other dental features used as identification characters in European shrews of the genus Sorex (Mammalia, Soricidae)

By E. Dannelid

Department of Zoology, University of Stockholm

Receipt of Ms. 4. 1. 1988

Abstract

The accessory medial tines on the incisors are regarded as one of the best identification characters of shrews of the genus *Sorex*. This character is here described for all non-USSR European species of the genus, together with some other characters concerning pigment patterns, sharpness of cusps of I_1, shape of A_1, position of lacrimal and mental foramina and colour of pigment, all having some identification value. It is proposed that some of these characters reflect adaptive specializations rather than phylogenetic relationships. Finally a key to identification of species based on dental characters described in this paper is constructed.

Introduction

Species identification of shrew skulls has for European species of the genus *Sorex* mostly been based on the following characters: measurements of skulls and teeth, shape and size of upper antemolars (following Reumer [1984] the teeth more commonly called unicuspids are here termed antemolars) and position of mental foramen in the lower jaw.

Recently several authors on North American and East Asian shrews (Heptner and Dolgov 1967; Hoffmann 1971; Hennings and Hoffmann 1977; Diersing and Hoffmeister 1977; Junge and Hoffmann 1981) have used the medial tines on the upper incisors as an effective identification character. The shape of the medial tines in European *Sorex* species has not previously been described in detail. Other characters, chiefly concerning pigment patterns, may also be used in identification. Some of these may be useful only for identification of certain species, while others are more generally applicable. It is possible to create a key to identification of European *Sorex* species using these characters, in some cases, however, combined with the position of the mental foramen, but without using the antemolars. This does not mean that the shape of the upper antemolars is a character of low identification value. Instead it is in most cases probably the easiest way to make an identification. However, using the "pigment-key" described here, it is also possible to identify specimens with damaged upper antemolars.

Material and methods

Skulls of nine shrew species of the genus *Sorex* were analyzed under a dissecting microscope. Geographical origin and number of skulls of each species is given in the table. The skulls were chiefly from young animals with teeth in good condition. (In old animals both the teeth and the pigment are worn to a considerable degree, which makes analyses difficult.) The following characters were studied: Presence or absence of medial tines on the upper incisors, their size and their position in the pigment field, pigmentation of hypocones on upper molars, position of lacrimal foramen, shape and pigmentation of the lower incisor, shape of the lower antemolar, pigment pattern on I_1–P_4, position of mental foramen and colour of the pigment.

Geographical origin and number of skulls studied of each species

Species	Number of skulls	Geographical area	Source
S. alpinus	28	Switzerland, Germany, Yugoslavia	1, 3
S. araneus	20	Sweden, Finland, Germany, Czechoslovakia	1
S. caecutiens	36	Sweden, Finland	1, 2
S. coronatus	26	Switzerland	3
S. granarius	13	Spain	3
S. isodon	31	Finland	2
S. minutissimus	8	Finland	2
S. minutus	28	Sweden, Germany	1
S. samniticus	15	Italy	3

Source: 1 = Swedish Museum of Natural History, Stockholm, Sweden; 2 = University of Oulu, Finland; 3 = Université de Lausanne, Switzerland.
Note: Apart from these forms, four additional species occur in the European part of USSR, *S. tundrensis* in the Pechora River valley etc. and the three Caucasian species *S. caucasicus, S. raddei* and *S. volnuchini.*

Results

Subgeneric characters

According to Hall (1981) and Junge and Hoffmann (1981) the majority of North American *Sorex*-species can be divided into the two subgenera *Sorex* and *Otisorex* (*Microsorex* is a monotypic subgenus characterized by the reduction of the third upper antemolar and will not be considered further.) The subgenus *Sorex* is characterized by the presence of a post-mandibular canal and by the absence of a pigmented ridge on the upper antemolars, *Otisorex* is conversely characterized by the opposite combination: absence of a post-mandibular canal and presence of a pigmented ridge on upper antemolars. No European *Sorex* showed any trace of a pigmented ridge on the upper antemolars. A postmandibular canal was present on at least one side (mostly on both), except in three skulls (one *S. coronatus* and two *S. samniticus*). The conclusion is that all European *Sorex* species belong to the subgenus *Sorex*.

Shape of upper incisors (frontal view)

The presence of accessory medial tines on the upper incisors (Fig. 1) was first noted by Heptner and Dolgov (1967) in the East Asian species *S. mirabilis*. They "proposed a new subgenus, *Ognevia* to accomodate what they believed to be important pecularities found in *S. mirabilis*" (citation from Hoffmann 1971). Since then it has been found that medial tines occur in many species of *Sorex* and that their presence or absence, size and position in the pigmented field is a very good identification character (Diersing and Hoffmeister 1977; Hennings and Hoffmann 1977; Junge and Hoffmann 1981). Another character, closely related to the shape of the medial tines is the shape of the tips of the incisors and their specing relative to each other. If the medial tines were situated low in the pigmented zone the free incisor tips (the area below the medial tines) were consequently short and also mostly parallel. However, if the tines were situated high up, the incisor tips were long and usually somewhat diverging.

In frontal view the first pair of upper antemolars may be more or less visible behind the incisors. They are clearly visible in *S. alpinus* and *S. samniticus*, less so in other species. Finally the colour of the pigment, how high the pigmented area rises on the incisor and if the upper border of the pigmented area on the first cusp on I^1 is straight or oblique may all be worth noticing.

Sorex araneus (Fig. 1a): Pigment dark, medial tines rather large, situated in the lower half of the pigmented area (sometimes as high as at the middle of this area), tips of incisors blunt, parallel, not diverging.

Sorex coronatus: Not distinguishable from *S. araneus*.

Sorex granarius (Fig. 1b): Pigment rather light, medial tines small to very small, situated in the lower half of the pigmented area, tips of incisors similar to *S. araneus*.

Sorex samniticus (Fig. 1c): Pigment intermediate, medial tines large, situated in the upper half of the pigmented area, tips of incisors were slightly more diverging than in most *S. araneus*.

Sorex caecutiens (Fig. 1d): Colour of pigment intermediate between *S. araneus* and *S. minutus*, medial tines very small to fairly large, usually situated near the middle of the pigmented area (but sometimes fairly deep in the lower half), tips of incisors diverging,

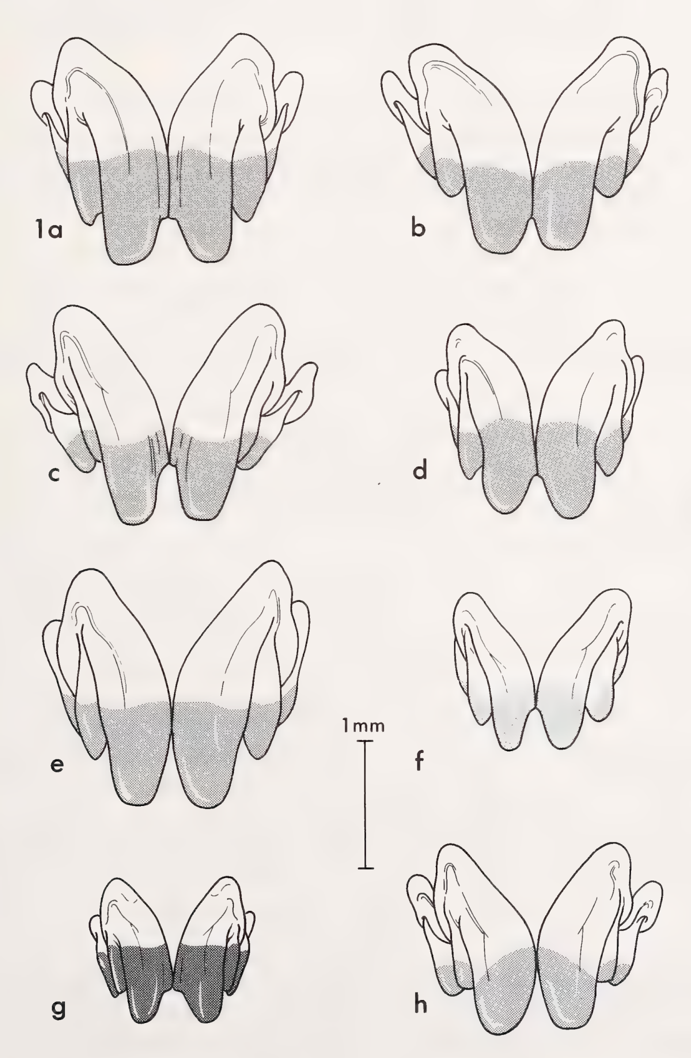


Fig. 1. Upper incisors of shrews in frontal view. a: *S. araneus;* b: *S. granarius;* c: *S. samniticus;* d: *S. caecutiens;* e: *S. isodon;* f: *S. minutus;* g: *S. minutissimus;* and h: *S. alpinus*

rather sharp-pointed, upper borderline of pigmented area straight to oblique (see *S. alpinus*).

Sorex isodon (Fig. 1e): Pigment intermediate, medial tines very small, situated in the uppermost part of the pigmented area, tips of incisors blunt, rather parallell to sligthly diverging.

Sorex minutus (Fig. 1f): Pigment light, medial tines rather large, situated in the upper half of the pigmented area, tips of incisors more sharp-pointed and diverging than in any other species.

Sorex minutissimus (Fig. 1g): Pigment very dark, medial tines very large, situated extremely low in the pigmented area, which made the tips of the incisors very short and rather blunt. This was the only species where the pigment cover rose as high as the dividing point between the first and second cusp of the incisor. It was also unique in that a small area of lighter pigment separated the pigmented and nonpigmented areas. These facts together with the elongated shape of the incisor makes *S. minutissimus* one of the easiest species to recognize.

Sorex alpinus (Fig. 1h): Pigment rather light, medial tines absent, tips of incisors blunt and parallel to slightly diverging. In this species the upper borderline of the pigmented area was clearly oblique, while in all other species it was relatively straight (some *S. caecutiens* had a borderline almost as oblique as *S. alpinus*). In frontal view the first antemolar was clearly visible behind the incisors in this species, a condition also found in *S. samniticus* but not in other European *Sorex* species.

Pigmented hypocones on upper molars

This character (Fig. 2) separates *S. araneus* and *S. coronatus* from all other species. In young *S. araneus* and *S. coronatus* the hypocones on M^1 and (usually) M^2 (and very rarely P^4 as well) were very weakly pigmented (in old animals the teeth are worn, and naturally the pigment on the hypocones is absent), while in all other species (even the related *S. granarius*) the hypocones were completely unpigmented.

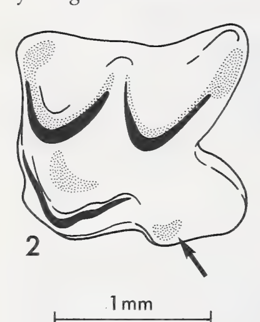


Fig. 2. Left M^1 of *S. araneus* showing pigmented hypocone (arrow)

Relative position of lacrimal foramen

Although not being of the same importance as the position of the mental foramen, the position of the lacrimal foramen relative to the first and second upper molar teeth is sometimes a useful taxonomic character (VAN ZYLL DE JONG 1980). Lacrimal foramen placed over:

1. central part of M^1 (mesostyle to between metacone and metastyle): *S. araneus, S. coronatus, S. granarius, S. samniticus, S. caecutiens.*
2. posterior part of M^1 (metacone to metastyle): *S. minutus, S. minutissimus, S. isodon.*
3. between M^1 and M^2 or over parastyle of M^2: *S. alpinus.*

Shape of I_1

The shape of the lower incisor can in some cases be used to distinguish between species. Characters worth noticing are the shape and size of the cusps and the distribution of the pigmented area (Fig. 3). All European *Sorex* species had four cusps, but there was a great difference between the sharp, triangular cusps of *S. minutus* and the blunt, rounded cusps of *S. araneus. S. minutissimus* also had a clearly recognizable cusp-pattern. *S. minutus* was

the only species showing really sharp-pointed cusps; while several species (*S. granarius*, *S. samniticus* and *S. alpinus*) had blunter cusps than *S. araneus*.

The relative size of the cusps may also be important. The third cusp was mostly larger, often considerably so, than the fourth. However, in *S. minutus* and *S. alpinus* the third and fourth cusps were of approximately the same size, even though the fourth appeared smaller because it was less pigmented.

In labial view the pigment on the lower part of the tooth reached backwards to a point approximately between first and second cusps in most species, while in *S. minutissimus* it reached further back, between the second and third cusps, which simply means that I_1 had a larger pigmented area in this species. In *S. minutus, S. minutissimus, S. alpinus, S. granarius* and *S. samniticus* all four cusps were usually included in a continuous pigmented area, while in *S. araneus* and *S. coronatus* the pigment of the fourth cusp were often isolated from the main pigmented area. In *S. caecutiens* and *S. isodon* the third cusp were also sometimes isolated in this way.

Shape of A_1

In *S. araneus* and *S. coronatus* this tooth was more or less triangular in shape, while in other species it was prolonged and sometimes showed a prominent posterior ridge (Fig. 3). This ridge was usually unpigmented but in some species *(S. minutus, S. minutissimus, S. samniticus)* it was sometimes pigmented. In *S. alpinus* the ridge was pigmented and transformed into a cusp, which gave this species a two-cusped A_1. It is often stated that *S. alpinus* is the only European *Sorex* showing this condition, however, specimens of both *S. samniticus* and *S. minutissimus* with a two-cusped A_1 were found. In these cases the second cusp was much smaller than and closer to the first cusp compared with what was found in *S. alpinus* (Fig. 3c–d).

Pigment pattern on I_1–P_4

The border between the pigmented and unpigmented areas of the first three teeth in the lower jaw is sometimes useful for distinguishing species. Three patterns can be recognized:

1. The "*araneus*-pattern" (Fig. 3a): The border between pigmented and unpigmented areas runs continuously on I_1, A_1 and P_4, without apparent breaks. This condition was found in *S. araneus* and *S. coronatus.*
2. The "*minutus*-pattern" (Fig. 3b): The border between pigmented and unpigmented areas runs continuously on I_1 and A_1 but probably due to the non-triangular shape of the latter tooth, starts much higher on P_4, leaving a distinct gap. This condition was found in *S. minutus*. In *S. granarius, S. samniticus, S. caecutiens, S. isodon* and *S. minutissimus* the pattern was often somewhat intermediate between the two patterns described above.
3. The "*alpinus*-pattern" (Fig. 3d): The border between pigmented and unpigmented areas runs continuously on I_1 and A_1 but on P_4 it starts much lower, almost from the basal part of the tooth, and then runs in a semi-circular fashion over P_4. This was found only in *S. alpinus.*

Relative position of mental foramen

The position of the mental foramen relative to P_4–M_1 is commonly used in field guides etc. but not always accurately. In this study the following positions were found (Fig. 3):

S. alpinus: below P_4 or sometimes below P_4–M_1.

S. isodon: below P_4–M_1 or below the anterior part of the trigonid of M_1, seldom centrally placed below the trigonid of M_1.

S. minutus: below the anterior part of the trigonid of M_1.

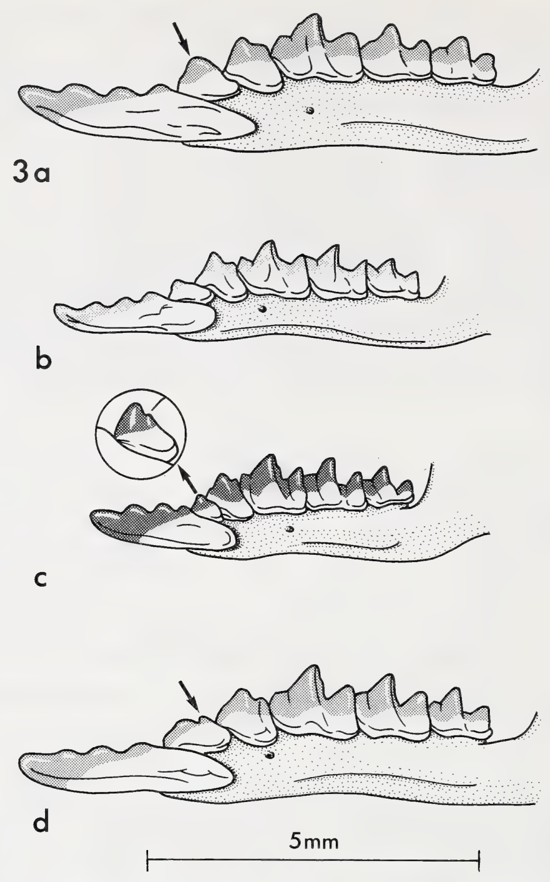


Fig. 3. Left lower jaw of shrews in labial view; a: *S. araneus* showing triangular A_1 (arrow) and typical „*araneus*"-pigment pattern on I_1–P_4; b: *S. minutus* showing sharp cusps on I_1 and typical „*minutus*"-pigment pattern on I_1–P_4; c: *S. minutissimus* (and inserted a two-cusped A_1 which is not normal for the species); d: *S. alpinus* showing a two-cusped A_1 (arrow) and „*alpinus*"-pigment pattern on I_1–P_4. The mental foramen is visible under P_4–M_1

S. araneus, S. coronatus, S. caecutiens, S. granarius and *S. samniticus:* below the trigonid of M_1, relatively centrally placed.

S. minutissimus: below the trigonid-talonid of M_1.

Colour of pigment

The colour (actually the degree of darkness/lightness) of the pigment has already been reviewed in the section dealing with the upper incisors. What is said there is also true for the pigment generally, *S. minutus* has the lightest pigment, *S. minutissimus* the darkest and the other species are intermediate. It should be borne in mind that the pigment is generally darker on the lower incisor than further back in the lower jaw.

The red colour of the pigment is due to the presence of iron (Dötsch and von Koenigswald 1978; Vogel 1984). According to Dötsch and von Koenigswald (1978) the lower incisor shows the greatest quantity of iron in *S. araneus*. The same may be true for most species of *Sorex*.

Discussion

The medial tines on the upper incisors are a good specific identification character. The question is, however, if similarities in the characters described in this work reflect taxonomic relationships between species or are results of adaptations to a similar way of life. The parallelism may occur is demonstrated by the two smallest species in the Old and New World, *S. minutissimus* and *S. (Microsorex) hoyi* respectively. Seen in frontal view the incisors of these two pygmy species are very similar (c.f. Fig. 1g in this work and Fig. 4 in JUNGE and HOFFMANN 1981), with their large medial tines placed low down on the teeth and their very dark pigment. The front part of the jaw is shortened in both species, but the effect of this shortening on the upper antemolars is quite distinct in the two forms. In *S. hoyi* the third and the fifth antemolars are reduced so that the animal at a quick glance appears to have only three upper antemolars. In *S. minutissimus* all five antemolars are well-developed but situated close together. Since these species are not closely related, these similarities must be adaptations to a similar way of life.

The best available evidence for phylogenetic relationships between European *Sorex* is probably cytological. Of the nine species described in the present paper, three (*S. araneus, S. coronatus* and *S. granarius*), belong to the *Sorex araneus/arcticus*-group, characterized by two-armed x-chromosomes and (in males) two y-chromosomes (HAUSSER et al. 1985). *S. samniticus,* although superficially similar has a completely different karyotype (GRAF et al. 1979) and is also electrophoretically different (CATZEFLIS, thesis 1984). It is interesting to note that *S. araneus, S. coronatus* and *S. granarius* all have medial tines situated in the lower half of the pigmented area while *S. samniticus* has them in the upper part. However, this does not amount to state that the *S. araneus/arcticus*-group is characterized by medial tines located in the lower part of the pigmented field of the incisors. Firstly the shape of the medial tines is not known in Asian members of this group, and the North American forms have, as indicated by JUNGE and HOFFMANN (1981 p. 20) the medial tines high on the anterior face of I^1. Secondly many other species (in Europe *S. minutissimus*) have medial tines placed low on the incisors.

Even though the phylogenetic value of some characters mentioned in this work seems to be limited, the characters uniting *S. araneus* and *S. coronatus* (pigmented hypocones on M^1–M^2, perhaps also the triangular A_1) appear to confirm that these species are closely related.

If the characters mentioned are instead regarded as ecological adaptations the question arises: to what? What does it mean for example if a shrew has dark or light tooth pigment?

As the pigment is iron-containing, teeth with dark pigment are probably more resistant to wear. It is generally agreed that wear of teeth in shrews is chiefly accomplished by chewing. The shrew dentition comprises two functional parts: a front part containing incisors and antemolars and a back part consisting of the molariform teeth (DÖTSCH 1985; MALMQUIST, pers. comm.). The front part chiefly functions as a pair of tweezers when the shrew is catching the prey, while the back part is involved in chewing. Catching the prey probably causes less wear than chewing it. Still, the lower incisor is the most heavily pigmented tooth at least in *S. araneus* (DÖTSCH and VON KOENIGSWALD 1978). Could there be any other use for heavily pigmented incisors apart from dealing with sclerotized invertebrates?

It is well known that many species of shrews spend much time underground in burrows, self made or (for smaller species like *S. hoyi*) even insect-tunnels. If the incisors are involved in removing stones etc. from tunnels (CROWCROFT 1957) it would obviously be valuable to have heavily pigmented incisors. It might also be advantageous to have large medial tines placed very low on the incisors to provide a more efficient digging apparatus (compare fig. 1a and 1f). If this is true, we would expect a correlation between dark

pigment and large medial tines located low on the incisors. This might be true because *S. araneus* has darker pigment than *S. minutus* and also medial tines situated lower.

S. minutissimus has the largest (at least in relative size) and lowest positioned medial tines of all species and also the darkest pigment. It is also true that *S. araneus* spends more time underground than *S. minutus* (Croin Michielsen 1966). It should be expected that *S. minutissimus* has an even more subterranean behaviour.

The only species showing extensive variability in position of medial tines was *S. caecutiens*. Out of 36 skulls, 28 showed medial tines situated at the middle of the pigmented area or a little below, while 5 had the medial tines placed low in the pigment (the remaining 3 had damaged incisors). This may be due to the fact that *S. caecutiens* is an intermediate form also in body size. The Scandinavian species are ranked in order of decreasing size as follows: *S. isodon* – *S. araneus* – *S. caecutiens* – *S. minutus* – *S. minutissimus*. In the extremes *S. isodon* and *S. minutissimus* no variation at all could be observed in medial tines, and in *S. araneus* and *S. minutus* the variation was only minute. Having intermediate size, *S. caecutiens* could perhaps occupy the niche of *S. araneus* in absence of that species, while in the presence of *S. araneus* but absence of *S. minutus* it could tend so shift to the niche of *S. minutus* as suggested by Hanski and Kuitunen (1986). This might produce variation in the position of the medial tines. It might be argued that considerable intraspecific variation in the position of the medial tines renders this character useless as a systematic character, however, in no other species was there any significant variation.

S. minutus has sharp cusps on the lower incisor, while those of *S. sinalis, S. caecutiens* and *S. minutissimus* are blunter, those of *S. araneus* and *S. coronatus* still blunter and those of *S. granarius, S. samniticus* and *S. alpinus* finally extremely low and blunt. There is much more individual variation in this character than in the position of medial tines, which may be due to tooth wear.

One observation that might be of ecological importance is that *S. minutus* shows much sharper cusps on I_1 than any other European *Sorex*. This is probably not due to dealing with more chitinized prey than other species, since this is contradicted by the light pigment of the teeth. According to Pernetta (1976), *S. minutus* ate adult Coleoptera, Opiliones, Araneae and larvae (in that order) while the more blunt-cusped *S. araneus* ate earthworms, adult Coleoptera and Opiliones, and only to a lesser degree larvae and spiders. *S. minutus* does not eat earthworms which form a large part of the diet of *S. araneus* (Churchfield 1984). The sharp cusps on I_1 of *S. minutus* may give a better hold on to the prey during the capture. *S. minutus* does not do much digging and may therefore maintain sharper cusps on I_1 than for example, *S. araneus*.

Key to identification of species

1. Unpigmented hypocones on M^1–M^2 (Fig. 2), A_1 not triangular (Fig. 3b–d) 2

1a. Pigmented hypocones on M^1–M^2 (Fig. 2), A_1 triangular (Fig. 3a) . . . . *S. araneus/S. coronatus* (not distinguishable using this key)

2. Medial tines present on I^1 (may be small), upper border of pigment on I^1 seen in frontal view mostly straight, A_1 one-cusped, not "alpinus-pigment pattern" on I_1–P_4 3

2a. Medial tines on I^1 absent (Fig. 1h), upper border of pigment on I^1 seen in frontal view clearly oblique, A_1 two-cusped (S. samniticus and S. minutissimus might rarely have a two-cusped A_1 but it looks different, see Fig. 3c), "alpinus-pigment pattern" on I_1–P_4 (Fig. 3d) . . . . *S. alpinus*

3. Medial tines on I^1 in upper half of pigmented area 4

3a. Medial tines on I^1 in lower half of pigmented area 7

4. Mental foramen under the middle of the trigonid of M_1 5

4a. Mental foramen more anteriorly 6

5. Tips of incisors parallel, medial tines mostly high up in the pigmented area (Fig. 1c) ... *S. samniticus*
5a. Tips of incisors diverging, medial tines mostly near the middle of the pigmented area (Fig. 1d) ... *S. caecutiens*
6. Pigment darker, medial tines small, tips of incisors rather parallel, blunter, cusps on I_1 rather blunt (Fig. 1e) ... *S. isodon*
6a. Pigment lighter, medial tines rather large, tips of incisors diverging, sharper, cusps on I_1 sharp (Fig. 1f) ... *S. minutus*
7. Pigment very dark, medial tines on I^1 large (Fig. 1g) ... *S. minutissimus*
7a. Pigment light, medial tines on I^1 not very large ... 8
8. Tips of incisors more parallel, medial tines clearly in the lower half of the pigmented area (Fig. 1b) ... *S. granarius*
8a. Tips of incisors more diverging, medial tines mostly near the middle of the pigmented area, only rarely further below (Fig. 1d) ... *S. caecutiens*

Note: The difference between 8 and 8a is very slight when *S. caecutiens* has low placed medial tines but since the two species occur in widely separated geographical areas the risk for confusion should seldom occur.

Acknowledgements

I wish to express my gratitude to the Swedish Museum of Natural History, to Prof. SEPPO SULKAVA, Oulu, and to Prof. JACQUES HAUSSER, Lausanne for loaning me the material. I also wish to thank Prof. BO FERNHOLM, Stockholm, Dr. LARS WERDELIN, Stockholm and Dr. MATS MALMQUIST, Uppsala for critical comments on the manuscript. Finally I wish to thank Ms. BIBBI MAYRHOFER for helping me with the illustrations.

Zusammenfassung

Mediale Pfeiler an den oberen Schneidezähnen und andere Zahnmerkmale als Hilfe bei der Bestimmung europäischer Spitzmäuse der Gattung Sorex (Mammalia, Soricidae)

Die akzessorischen medialen Pfeiler (accessory medial tines) an den oberen Schneidezähnen gelten als wichtiges Merkmal zur Bestimmung von Spitzmäusen der Gattung *Sorex*. Dieses Merkmal wird hier an allen neun Arten untersucht, die in Europa außerhalb von Rußland vorkommen. Außerdem werden Verteilung und Intensität des Zahnpigments, die Gestalt der beiden Zähne I_1 und A_1 im Unterkiefer, die Lage des Foramen lacrimale und des Foramen mentale beschrieben. Die adaptive Bedeutung dieser Merkmale wird diskutiert. Ein auf diesen Kennzeichen aufbauender Bestimmungsschlüssel für die neun *Sorex*-Arten wird angegeben.

References

CHURCHFIELD, S. (1984): Dietary separation in three species of shrew inhabiting water-cress beds. J. Zool. London **204**, 211–228.
CROIN MICHIELSEN, N. (1966): Intraspecific and interspecific competiton in the shrews *Sorex araneus* and *S. minutus* L. Archives Neerlandaises de Zoologie **17**, 73–174.
CROWCROFT, P. (1957): The life of the shrew. London: Stellar Press.
DIERSING, V. E.; HOFFMEISTER, D. F. (1977): Revision of the shrews *Sorex merriami* and a description of a new species of the subgenus *Sorex*. J. Mammalogy **58**, 321–333.
DÖTSCH, C. (1985): Masticatory function in shrews (Soricidae). Acta Zool. Fennica **173**, 231–235.
DÖTSCH, C.; V. KOENIGSWALD, W. (1978): Zur Rotfärbung von Soricidenzähnen. Z. Säugetierkunde **43**, 65–78.
GRAF, J.-D.; HAUSSER, J.; FARINA, A.; VOGEL, P. (1979): Confirmation du statut specifique de *Sorex samniticus* Altobello, 1926 (Mammalia, Insectivora). Bonner Zool. Beitr. **30**, 14–21.
HALL, E. R. (1981): The mammals of North America. 2nd ed. New York: Wiley.
HANSKI, I.; KUITUNEN, J. (1986): Shrews on small islands: epigenetic variation elucidates population stability. Holarctic ecology **9**, 193–204.
HAUSSER, J.; CATZEFLIS, F.; MEYLAN, A.; VOGEL, P. (1985): Speciation in the *Sorex araneus* complex (Mammalia: Insectivora). Acta Zool. Fennica **170**, 125–130.

Hennings, D.; Hoffmann, R. S. (1977): A review of the taxonomy of the *Sorex vagrans* species complex from western North America. Occ. paps. Mus. nat. hist. Univ. Kansas **68,** 1–35.

Heptner, V. G.; Dolgov, V. A. (1967): O sistematicheskom polozhenni *Sorex mirabilis* Ognev, 1937 (Mammalia, Soricidae). Zool. Zhur. **56,** 1419–1422.

Hoffmann, R. S. (1971): Relationships of certain Holarctic shrews, genus *Sorex*. Z. Säugetierkunde **36,** 193–200.

Junge, J. A.; Hoffmann, R. S. (1981): An annotated key to the longtailed shrews (genus *Sorex*) of the United States and Canada, with notes on Middle American *Sorex*. Occ. paps. Mus. nat. hist. Univ. Kansas **94,** 1–48.

Pernetta, J. C. (1976): Diets of the shrews *Sorex araneus* L. and *Sorex minutus* L. in Wytham grasslands. J. Anim. Ecol. **45,** 899–912.

Reumer, J. W. F. (1984): Ruscinian and early pleistocene Soricidae (Insectivora, Mammalia) from Tegelen (the Netherlands) and Hungary. Scripta Geol. **73,** 1–173.

van Zyll de Jong, C. G. (1980): Systematic relationships of woodland and prairie forms of the common shrew, *Sorex cinereus cinereus* Kerr and *S. c. haydeni* Baird in the Canadian prairie provinces. J. Mammalogy **68,** 66–75.

Vogel, P. (1984): Verteilung des roten Zahnschmelzes im Gebiß der Soricidae (Mammalia, Insectivora). Rev. suisse Zool. **91,** 699–708.

Author's address: Erland Dannelid, Department of Zoology, University of Stockholm, S-106 91 Stockholm, Sweden

Z. Säugetierkunde 54 (1989) 215–222

ISSN 0044-3468

Chromosome studies in three genera of Australian vespertilionid bats and their systematic implications

By Marianne Volleth and C. R. Tidemann

Department of Human Genetics, University of Erlangen-Nürnberg, FRG, and Department of Forestry, Australian National University, Canberra, Australia

Receipt of Ms. 13. 1. 1988

Abstract

Karyologically studied were four Australian species of vespertilionid bats, i. e. *Nyctophilus gouldi, Chalinolobus morio, Pipistrellus (Vespadelus) vulturnus* and *P. (V.) sagittula.* All species possess a karyotype of 44 chromosomes showing a banding pattern, which bears great resemblance to that of the genus *Myotis.* However, each genus studied here can be distinguished from the others by means of small differences. The karyological similarities of these morphologically very different genera are surprising and provide indications of the ancestral vespertilionid karyotype. Concerning the systematic position of *P. vulturnus* and *P. sagittula,* formerly placed in the genus *Eptesicus,* both the morphology of bacula (Hill and Harrison 1987) and the chromosomal characteristics suggest that these species be removed from *Eptesicus* and belong to the taxon *Vespadelus,* which at least constitutes a separate subgenus of *Pipistrellus.*

Introduction

For 55 million years Australia has been an isolated continent. During this time a great number of endemic mammal species evolved, many of which belong to the Marsupialia. Among bats, although they reached Australia from Indonesia as late as 15 Million years ago (Archer and Clayton 1984), there can be found not only endemic species but also endemic genera. In the family Vespertilionidae one subfamily, i. e. Nyctophilinae, and several genera, e. g. *Chalinolobus* and *Scotorepens,* are endemic to the Australian region. This paper describes the karyotypes of *Nyctophilus gouldi,* which represents the endemic subfamily, Nyctophilinae, and *Chalinolobus morio,* a member of an endemic genus. In Australia there are also endemic species of genera, which have a worldwide distribution, as e. g. *Pipistrellus* and *Myotis.* The present paper deals with two endemic vespertilionid species, *Pipistrellus vulturnus* and *P. sagittula* which had been placed in the genus *Eptesicus* due to the absence of the second upper premolar (pm^2). This tooth is present in most species of the otherwise morphologically very similar genus *Pipistrellus.* However, Heller and Volleth (1984) recommended that these Australian species should be removed from *Eptesicus* on account of the *Pipistrellus*-like shape of the baculum, and Hill and Harrison (1987), after examination of the bacula of a large number of *Eptesicus* and *Pipistrellus* species, placed the Australian species in a separate subgenus of *Pipistrellus,* i. e. *Vespadelus.*

The karyotypic study presented here supports this separation. It also shows that the karyotypes of all species examined are very similar and come close to the proposed ancestral karyotype of the Vespertilionidae.

Materials and Methods

The animals were collected from free-living populations in Australia, and the specimens are now deposited in the Senckenberg-Museum, Frankfurt/Main (accession numbers in parenthese).

Specimens examined: *Nyctophilus gouldi* Tomes, 1858, Bull's Head, Australian Capital Territory,

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5404-0215 $ 02.50/0

34°24′S, 148°50′E (male, SMF 64967), *Chalinolobus morio* Gray, 1841, Bull's Head, (male SMF 64969, female SMF 64968), *Pipistrellus (Vespadelus) vulturnus* (Thomas 1914), Durras, New South Wales, 35°39′S, 150°20′E (male SMF 64970, female SMF 64971) and *Pipistrellus (Vespadelus) sagittula* (McKean, Richards and Price 1978), Durras (males SMF 64973, and 64974).

Metaphases were obtained from fibroblast cultures of heart and lung tissues. (Culture conditions see Volleth 1987). The slides were stained according to the following procedures. Sequential stainings Q-AgNOR (for details see Volleth 1987) and Q-CBG (C-banding according to Sumner [1972] with slight modifications, see Volleth and Yong [1987]), double staining with chromomycin A and DAPI (Schweizer 1980) and G-banding according to Seabright (1971), using Giemsa's stain instead of Leishman's. Replication patterns were obtained after RBG-banding (Camargo and Cervenka 1980) of BrdU-substituted cells. The chromosome arms were numbered according to Bickham (1979a).

Results

All species examined here possess 44 chromosomes. A comparison of the G-banded karyotypes is shown in fig. 1. On the whole, the banding scheme of Bickham (1979a), established for American *Myotis* species, can be used for chromosome identification, but in the following cases there were differences from the *Myotis* scheme. In *Nyctophilus gouldi* and *Chalinolobus morio*, chromosome 7 lacks the euchromatic short arm, present in *Myotis* species. Chromosome 15 possesses a nucleolus organizer region (NOR) near the centromere in all species examined here. Chromosome 12 and the X chromosome, which differ slightly from those of *Myotis*, are similar to those of the European *Pipistrellus* species (Volleth, unpubl. results). An important difference concerns chromosome 11. In contrast to the situation in *Myotis*, where the clear-cut G-negative band is located only a short distance from the middle of the chromosome, the same band is found more terminally in the Australian bats (see fig. 2). Therefore, amongst the European vespertilionid species, *Pipistrellus (Hypsugo) savii* comes closest to the Australian species treated here.

Description of the karyotypes

Nyctophilus gouldi: A G-banded karyotype (2n = 44, FN = 50) is shown in fig. 1. The subtelocentric Y chromosome is late-replicating, mainly heterochromatic and as large as chromosome 24. One homologue of pair 15 shows a small heterochromatic band between the centromere and the secondary constriction, although this might be an individual feature of the specimen examined.

Chalinolobus morio: The G-banded karyotype is shown in fig. 1 (2n = 44, FN = 50). The main difference from the karyotype of *Nyctophilus* concerns the third smallest chromosome. In *Chalinolobus* it is larger, due to the addition of G-positive heterochromatin in the proximal region (see fig. 3a). Only about 30 % of the chromosome consists of early replicating euchromatin. This chromosome is probably not homologous to chromosome 23 of the other species, but to chromosome 24 or 25. Because of the difficulties in comparing such small chromosomes, the three smallest pairs of *Chalinolobus morio* were arranged according to size. After silver staining, both individuals examined showed double NORs on one homologue of chromosome 15 in well extended metaphases (see fig. 3b). This is not regarded as a species-specific feature, but has also been found in other species with secondary constrictions (e. g. *Eptesicus nilssonii* and *E. serotinus*, Volleth, unpubl. data). In addition, a weak intercalar C-band could be seen on chromosome 13 near the centromere in most metaphases of both specimens. The submetacentric Y chromosome is the same size as the smallest autosome and is late-replicating and mainly heterochromatic.

Pipistrellus (Vespadelus) vulturnus: A G-banded karyotype is shown in fig. 1. Both *Pipistrellus* species examined possess non-heterochromatic short arms on chromosomes 7 and 13 and therefore the fundamental number is 54 instead of 50 (fig. 4). In both cases the short arm is early replicating, chromomycin A positive, G- and C-negative and therefore

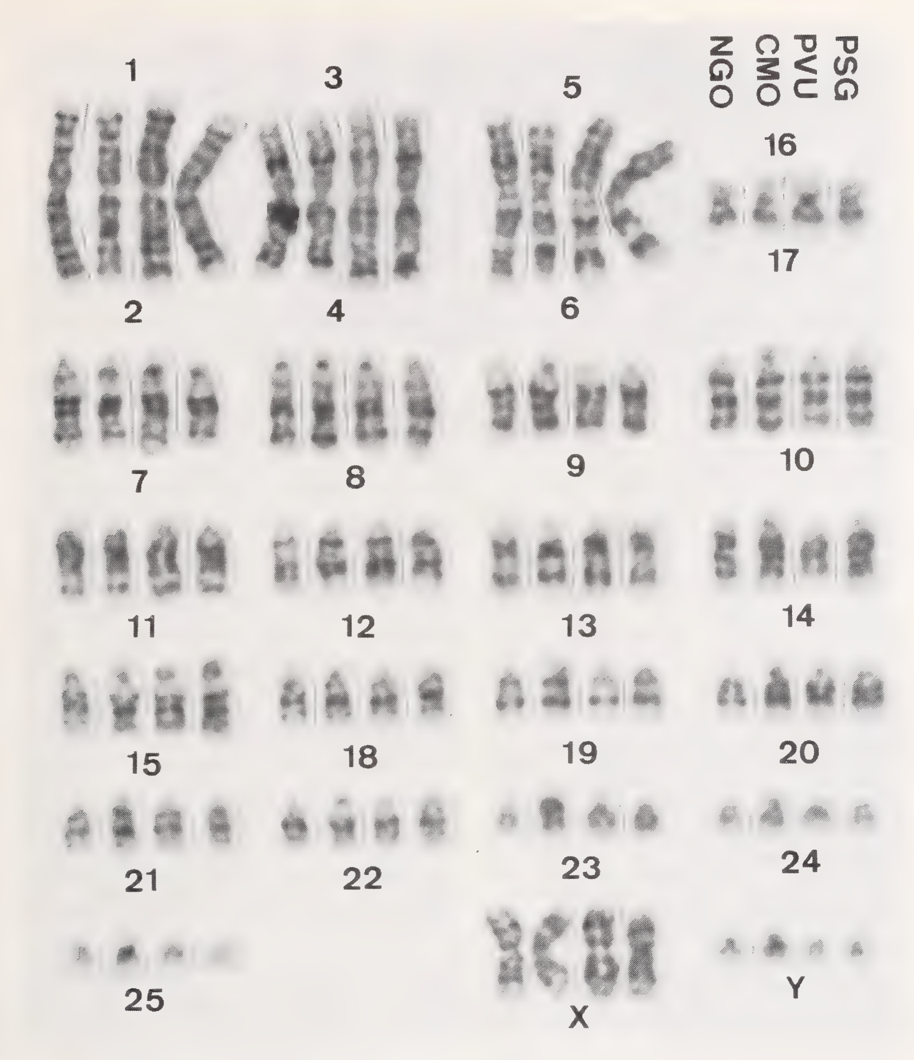


Fig. 1. Comparison of G-banded karyotypes, from left to right: *Nyctophilus gouldi* (NGO), *Chalinolobus morio* (CMO), *Pipistrellus vulturnus* (PVU), and *Pipistrellus sagittula* (PSG). All chromosomes shown for each species belong to the same metaphase, except for *P. vulturnus,* where the Y chromosome belongs to the male specimen and the remaining chromosomes to the female. Numbering according to BICKHAM (1979a)

probably euchromatic. In *P. vulturnus* the centromeric areas of chromosomes 7 and 13 show distinct heterochromatic dots after C-banding, as the remaining chromosomes (fig. 5a). In both chromosomes, a small pericentric inversion could have lead from the situation present in *Chalinolobus* and *Nyctophilus* to that in the subgenus *Vespadelus* (or vice versa).

The very small submetacentric Y chromosome replicates late and is slightly heterochromatic.

P. (Vespadelus) sagittula: In contrast to *P. vulturnus,* the centromeric areas of chromosomes 7 and 13 are not or only very slightly stained after C-banding (fig. 5b). The existence of short arms, however, can be clearly stated in G- and RBG-banded metaphases

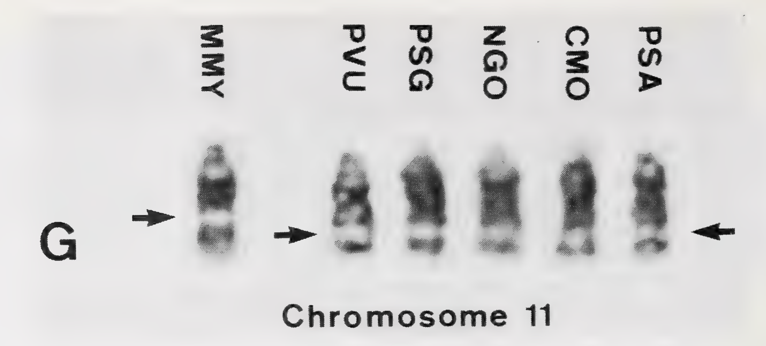


Fig. 2. G-banding of chromosome 11 of *Myotis myotis* (MMY), *P. vulturnus* (PVU), *P. sagittula* (PSG), *Nyctophilus gouldi* (NGO), *Chalinolobus morio* (CMO) and *Pipistrellus savii* (PSA). The arrows point to the clear-cut G-negative band, which in the Australian species and *P. savii* is situated more terminally than in *Myotis*

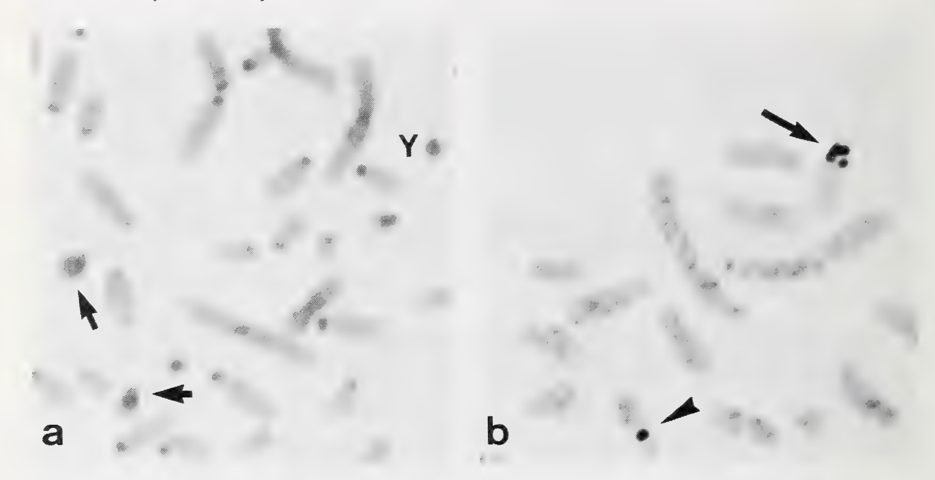


Fig. 3. Partial C-banded (a) and AgNOR-stained (b) metaphases of *Chalinolobus morio*. In (a) the arrows indicate chromosome 23, which largely consists of C-positive material. In (b) the arrow points to a double NOR, and the arrowhead to a normal NOR on chromosome 15

(fig. 4). The remaining chromosomes show distinct heterochromatic dots at the centromeres. On one homologue of chromosome 15 of one of the two males examined there is an unusually large secondary constriction (SC), which after silver staining appeared as a double NOR in some metaphases. The same chromosome shows a small heterochromatic band distal to the SC after C-banding, and in some metaphases of both specimens, chromosome arm 16 had a darker appearance after C-banding than the remaining euchromatic regions. The remaining chromosomes, including the Y, are similar to those of *P. vulturnus*.

Discussion

The representatives examined here of the genera *Nyctophilus, Chalinolobus* and the *Pipistrellus* subgenus *Vespadelus* are morphologically very distinct. *Nyctophilus* especially shows many morphological specializations (e. g. large ears, joined together above the

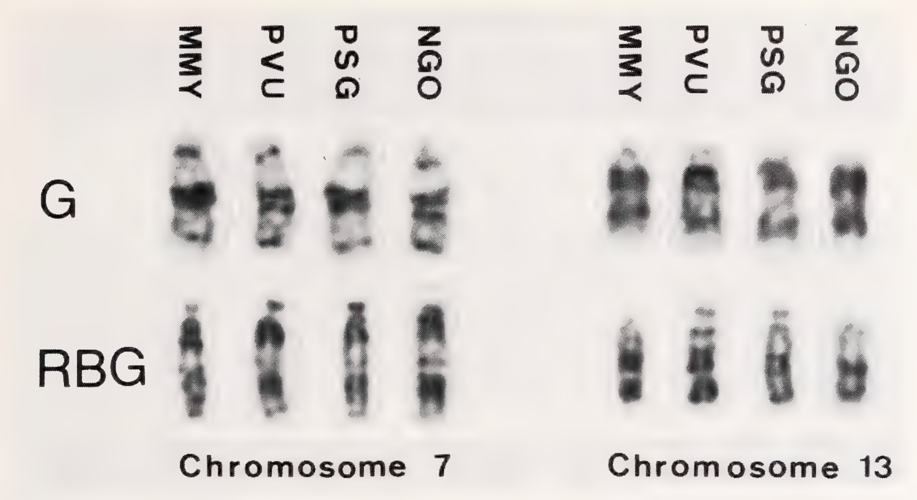


Fig. 4. Comparison of G- and R-banded chromosomes 7 and 13 from *Myotis myotis* (MMY), *Pipstrellus vulturnus* (PVU), *P. sagittula* (PSG) and *Nyctophilus gouldi* (NGO). Chromosome 7 possesses a small short arm in MMY, PVU and PSG, as can best be shown by R-banding. In chromosome 13 there exists a short arm only in PVU and PSG

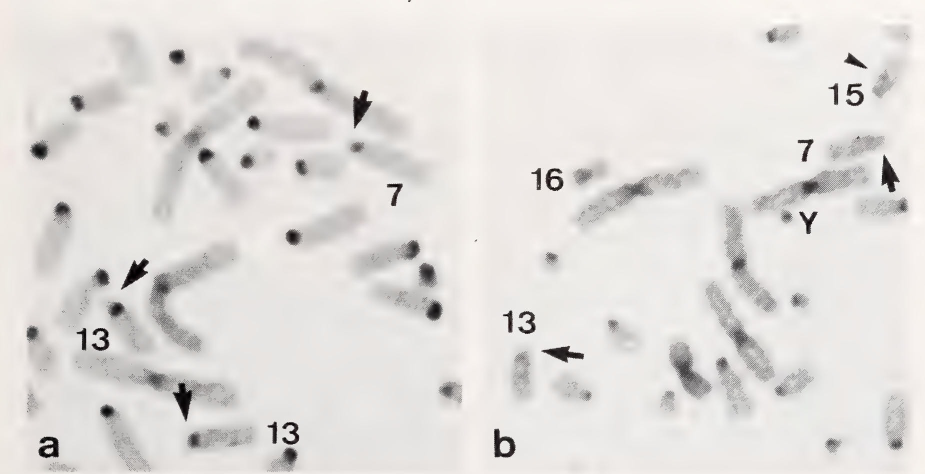


Fig. 5. Partial C-banded metaphases of *P. vulturnus* (a) and *P. sagittula* (b). The arrows point to the short arms present on chromosomes 7 and 13. In *P. sagittula* the centromeric heterochromatin of these chromosomes is not or only slightly stained. Additionally, the small interstitial C-band on chromosome 15 is marked by an arrowhead and chromosome arm 16 and the Y chromosome are indicated (see text)

forehead, characteristic noseleaf), which have caused most authors (see Hill and Harrison 1987) to establish a separate subfamily, Nyctophilinae.

It is thus very surprising that all species have almost identical karyotypes (2n = 44), which bear great resemblance to that of *Myotis* (Bickham 1979a; Volleth 1987). An important difference, however, can be found on chromosome 11. In the species examined and in *Pipistrellus (Hypsugo) savii* (Volleth, unpubl. results) the clear-cut G-negative region is located more distally than in *Myotis* and the remaining European species of *Pipistrellus (P. pipistrellus, kuhlii* and *nathusii*), probably due to a paracentric inversion. At

the moment we cannot decide which of these two forms of chromosome 11 is ancestral and which is derived. Apart from that the karyotype of *Chalinolobus morio* is characterized by heterochromatin addition in a small autosome and those of the *Pipistrellus* species are characterized by short arms on chromosomes 7 and 13 (see below).

Systematic position of the Australian *Pipistrellus*

The Australian species *vulturnus, sagittula, regulus, pumilus* and *douglasi* have been placed in the genus *Eptesicus* because they lack the second upper premolar. But it has been proposed earlier, that they should be transferred to the genus *Pipistrellus* due to the clearly *Pipistrellus*-like shape of the baculum (Heller and Volleth 1984). This has now been done by Hill and Harrison (1987) after examination of the baculum shape of a large number of *Pipistrellus* and *Eptesicus* species. The results now obtained from karyological examination confirm these findings. *P. vulturnus* and *P. sagittula* possess 44 chromosomes and not 50 as the remaining *Eptesicus* species (Heller and Volleth 1984). Their karyotypes come closest to that of *Pip. (Hypsugo) savii* but otherwise show euchromatic short arms on chromosome 7 (also found in *Myotis*) and 13. It should be noted, that the species with a derived, shortened baculum, *P. sagittula,* lacks the heterochromatic centromeric dots in these chromosomes after C-banding.

These chromosomal and morphological differences justify at least the nomination of a separate subgenus of *Pipistrellus, Vespadelus* (Throughton 1943), as proprosed by Hill and Harrison (1987). The relationships within the bat-infesting mites of the genus *Pteracarus* give further indications, that these Australian species are related to *Pipistrellus* and *Nyctalus* (Uchikawa and Harada 1981).

Proposed ancestral karyotype of the Vespertilionidae

A karyotype comprising 44 chromosomes, as found in the species examined here, has also been found in several morphologically very distinct genera: in *Myotis* (for references see Zima & Horacek 1985; Bickham et al. 1986), *Nyctalus furvus* (Harada et al. 1982), and the European representatives of *Pipistrellus* (Zima 1982), all belonging to the Vespertilioninae, and in *Murina* (Murininae, Harada et al. 1987). Additionally, there are several species which share three large metacentric chromosomes (composed of the arms 1 to 6) with the above mentioned species: members of the genera *Vespertilio* (Fedyk and Ruprecht 1985; Volleth 1985), *Nyctalus* (Harada et al. 1982). *Lasiurus* (Bickham and Baker 1979), *Plecotus, Barbastella* and *Idionycteris* (Stock 1983; Volleth 1985), all subfamily Vespertilioninae. The karyotypes of these species could have evolved from the ancestral karyotype mainly by centric fusions. A representative of the subfamily Miniopterinae, *Miniopterus schreibersii,* possesses two of the three metacentrics in question (1/2 and 5/6, Bickham 1978). In our opinion therefore, it is highly probable, that a karyotype with 44 chromosomes comes very close to the ancestral karyotype of Vespertilionidae, as other authors have suggested previously (Ando et al. 1977; Bickham 1979b; Zima 1982). We consider that the *Eptesicus* karyotype (2n = 50) evolved from a karyotype composed of 44 chromosomes by centric fissions of the three large metacentric chromosomes (1–2, 3–4, 5–6). Considering the *Eptesicus* karyotype as the ancestral one and, as a consequence, assuming a course of evolution with only fusion events (Fedyk and Ruprecht 1983), would imply, that *Eptesicus* is a sister group to all the above mentioned subfamilies of Vespertilionidae and that all morphological similiarities with the genus *Pipistrellus* have to be regarded as convergent. We believe this to be rather improbable.

Acknowledgements

We are grateful to Prof. R. A. Pfeiffer, Dept. of Human Genetics, Prof. O. v. Helversen and Dr. K.-G. Heller, Dept. of Zoology, for critical reading of the manuscript. We would like to thank the Australian National Parks and Wildlife Service for the permission to collect and export the animals. Warm thanks are also due to Matthias Hennig for his help in transporting the bats.

Zusammenfassung

Analyse und systematische Bewertung des Karyotyps von drei australischen Vespertilioniden-Gattungen (Chiroptera: Vespertilionidae)

Die vier australischen Vespertilioniden-Arten *Nyctophilus gouldi, Chalinolobus morio, Pipistrellus (Vespadelus) vulturnus* und *Pipistrellus (Vespadelus) sagittula* besitzen alle einen diploiden Karyotyp mit 44 Chromosomen und einem Bandenmuster, das große Ähnlichkeit mit dem der Gattung *Myotis* aufweist. Jede Gattung kann jedoch anhand bestimmter Merkmale von den übrigen unterschieden werden. Die Übereinstimmungen im Chromosomensatz bei diesen morphologisch sehr verschiedenen Gattungen sind überraschend und geben einen wichtigen Hinweis auf den ursprünglichen Karyotyp der Vespertilionidae.

Die chromosomalen Befunde unterstützen die von Hill und Harrison (1987) aufgrund der Morphologie der Penisknochen vorgenommene Umstellung der beiden Arten *Pipistrellus vulturnus* und *P. sagittula* aus der Gattung *Eptesicus* in das Taxon *Vespadelus*, das mindestens eine eigene Untergattung von *Pipistrellus* darstellt.

References

Ando, K.; Tagawa, T.; Uchida, T. A. (1977): Considerations of karyotypic evolution within Vespertilionidae. Experientia **33**, 877–879.

Archer, M.; Clayton, G. (eds) (1984): Vertebrate zoogeography and evolution in Australasia. Carlisle: Hesperian Press.

Bickham, J. W. (1979a): Banded karyotypes of 11 species of American bats (genus *Myotis*). Cytologia **44**, 789–797.

– (1979b): Chromosomal variation and evolutionary relationships of vespertilionid bats. J. Mammalogy **60**, 350–363.

Bickham, J. W.; Baker, R. J. (1979): Canalization model of chromosomal evolution. Bull. Carnegie Mus. Nat. Hist. **13**, 70–84.

Bickham, J. W.; Hafner, J. C. (1978): A chromosomal banding study of three species of vespertilionid bats from Yugoslavia. Genetica **48**, 1–3.

Bickham, J. W.; McBee, K.; Schlitter, D. A. (1986): Chromosomal variation among seven species of *Myotis* (Chiroptera: Vespertilionidae). J. Mammalogy **67**, 746–750.

Camargo, M.; Cervenka, J. (1980): Pattern of chromosomal replication in synchronized lymphocytes. Hum. Genet. **54**, 47–53.

Fedyk, S.; Ruprecht, A. L. (1983): Chromosomes of some species of vespertilionid bats. I. Banding pattern of *Eptesicus serotinus* chromosomes. Acta theriologica **28**, 159–170.

– – (1985): Chromosomes of some species of vespertilionid bats. III. Banded chromosomes of *Vespertilio murinus* L. 1758. Nyctalus (N.F.) **2**, 119–126.

Harada, M.; Ando, K.; Uchida, T. A.; Takada, S. (1987): A karyological study on two Japanese species of *Murina* (Mammalia: Chiroptera). J. Mammal. Soc. Japan **12**, 15–23.

Harada, M.; Uchida, T. A.; Yosida, T. H.; Takada, S. (1982): Karyological studies of two Japanese noctule bats (Chiroptera). Caryologia **35**, 1–9.

Heller, K.-G.; Volleth, M. (1984): Taxonomic position of *"Pipistrellus societatis"* Hill, 1972 and the karyological characteristics of the genus *Eptesicus* (Chiroptera: Vespertilionidae). Z. zool. Syst. Evolut. forsch. **22**, 65–77.

Hill, J. E.; Harrison, D. L. (1987): The baculum in the Vespertilioninae (Chiroptera: Vespertilionidae) with a systematic review, a synopsis of *Pipistrellus* and *Eptesicus* and the descriptions of a new genus and subgenus. Bull. Brit. Mus. (Nat. Hist.) Zool. **52**, 225–305.

Schweizer, D. (1980): Simultaneous fluorescent staining of R-bands and specific heterochromatic regions (DA-DAPI bands) in human chromosomes. Cytogenet. Cell Genet. **27**, 190–193.

Seabright, M. (1971): A rapid banding technique for human chromosomes. Lancet 1971 **II**, 971–972.

Stock, A. D. (1983): Chromosomal homologies and phylogenetic relationships of the vespertilionid bat genera *Euderma, Idionycteris,* and *Plecotus.* Cytogenet. Cell Genet. **35**, 136–140.

Sumner, A. T. (1972): A simple technique for demonstrating centromeric heterochromatin. Exp. Cell Res. **75**, 304–306.

Uchikawa, K.; Harada, M. (1981): Evaluation of bat-infesting Myobiidae (Acarina, Trombidifor-

mes) as indicators in taxonomy and phylogeny of host bats (Chiroptera). Zoological Magazine **90**, 351–361.

Volleth, M. (1985): Chromosomal homologies of the genera *Vespertilio, Plecotus* and *Barbastella* (Chiroptera: Vespertilionidae). Genetica **66**, 231–236.

– (1987): Differences in the location of nucleolus organizer regions in European vespertilionid bats. Cytogenet. Cell Gen. **44**, 186–197.

Volleth, M.; Yong, H. S. (1987): *Glischropus tylopus*, the first known old-world bat with an X-autosome translocation. Experientia **43**, 922–924.

Zima, J. (1982): Chromosomal homology in the complements of bats of the family Vespertilionidae. II. G-band karyotypes of some *Myotis, Eptesicus* and *Pipistrellus* species. Folia zool. Brno **31**, 31–36.

Zima, J.; Horacek, J. (1985): Synopsis of karyotypes of vespertilionid bats (Mammalia: Chiroptera). Acta Universitatis Carolinae – Biologica **1981**, 311–319.

Authors' addresses: Marianne Volleth, Department of Human Genetics, University of Erlangen-Nürnberg, Schwabachanlage 10, D-8520 Erlangen, FRG and Dr. Chris R. Tidemann, Department of Forestry, Australian National University, GPO Box 4, Canberra, ACT 2601, Australia

Z. Säugetierkunde 54 (1989) 223–228

ISSN 0044-3468

A method to estimate the survival differences among overwintered Microtines: Cyclic *Clethrionomys rufocanus* (Sund.) at Kilpisjärvi, Finnish Lapland

By J. A. Viitala

Konnevesi Research Station, University of Jyväskylä, Konnevesi, Finnland

Receipt of Ms. 15. 10. 1987

Abstract

A method is given to calculate the Standardized Root Length (SRL) of molars. It can be used to examine the changes in age structure of overwintered *Clethrionomys* without grouping the animals in separate cohorts. The age structure of overwintered animals indicated by mean SRL reacted on many different environmental factors. The oldest animals survived best in conditions with increasing mortality and in interspecific competitive situations. Thus the mean SRL seems to be a sensitive indicator of increased mortality. The examination revealed one decline starting earlier in oligotrophic and oligo-mesotrophic heath woods, when the populations in eutrophic meadow woods were still unaffected, thus indicating possible causes of the decline. Resource competition between sexes during decline was indicated.

Introduction

The growth and morphology of the molar teeth have been used as bases for age determination in different *Clethrionomys* species (Koshkina 1955; Tupikova et al. 1968; Viitala 1971, 1977; Lowe 1971; Viro 1974; Perrin 1978; Wiger 1979). Reference animals of known age are needed to estimate the real growth rate of the molars in different circumstances (Viitala 1971, 1977; Lowe 1971; Perrin 1978). Reference materials have not been available in all studies, however (e.g. Koshkina 1955; Wiger 1979). This has resulted in some confusing interpretations.

There are no genital markers that can be used to estimate the possible survival differences in their second summer between animals reproducing in their season of birth and those remaining immature (Viitala 1977).

The aim of the present paper is to describe a method to estimate the changes in age structure and compare different populations of overwintered animals without sorting the animals in cohorts and to examine some social aspects of demographic changes in a cyclic population.

Material and methods

The material of the present study consists of 701 overwintered specimens of *Clethrionomys rufocanus* snap trapped among 2234 individuals of that species (c.f. Viitala 1977) collected during 55000 trap nights. The trappings were done 1964–1970 by the expedition headed by the late Prof. Olavi Kalela in arctic-alpine environment of Kilpisjärvi area both above and below the timber line (for a description of the area s. e.g. Kalela 1957 or Viitala 1977). As a reference material I have used 267 animals of known age reared in the Department of Zoology, University of Helsinki (Viitala 1977). Information on age structure changes was also obtained by extensive live trapping study in 1967–1970 (Viitala 1977) and 1972–1974 (Viitala 1980, 1984 and unpubl.). The snap trapped material was collected mostly by baited commercial mouse traps in optimal *C. rufocanus* habitats. Some was also obtained by bigger unbaited commercial rat traps as a by-broduct of lemming trappings in paludified or alpine habitats during the years 1968–1970. According to Kalela et al. (1971) such habitats are suboptimal to *C. rufocanus* which is a typical forest species. Densities obtained in lemming habitats were always

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5404-0223 $ 02.50/0

lower than those in optimal habitats (VIITALA 1977). Materials from these two types of trappings have been treated separately.

The age indicator used in the present study was the total root length of M^2 (Fig. 1) (HENTTONEN and VIITALA 1982). Because of the extensive variation of the neck length of the tooth the separate root length did not correlate well with age (VIITALA 1971, 1977). The standardized root length (SRL) was calculated on the basis of measured total root length, to represent the situation on 15th June using formula:

$$l_0 = l_1 + (t_0 - t_1)g$$

where l_0 is the root length on 15th June (SRL) and l_1 that at the date of capture, t_0 is the date 15th June and t_1 is the date of capture and g is the growth rate during breeding season i.e. 0.26 mm/month (VIITALA 1977). Thus the differences in mean SRL observed in different times of the breeding season or in different habitats are due to different age structure. The growth value 0.26 mm/month for breeding season was obtained both from 256 animals reared in the laboratory (VIITALA 1977) and in the wild during a time when live trapping revealed no changes in age structure. The tooth growth during overwintering was much slower (VIITALA 1977).

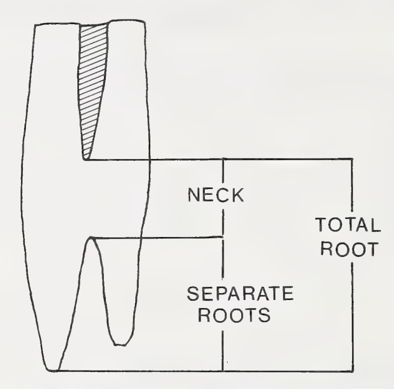


Fig. 1. The way to measure the root length of the second upper molar (according to HENTTONEN and VIITALA 1982) used in calculating the SRL. Because of the extensive variation in the neck length the separate root length did not correlate well with age

C. rufocanus may be the most suitable species for using SRL in a study on age structure since it has bigger teeth and more rapid growth of molar roots than the other *Clethrionomys* species and the root growth starts a month later at the age of two months (VIITALA 1977 and unpubl.). Hence it is easier to measure the age indicator. However, this kind of examination would be possible in other *Clethrionomys* species, too. It could probably be based also on other age indicators than molar root.

Results and discussion

Mean ages in different phases of cycle

In increasing and peak years 1968 and 1969 significant differences did not exist in mean SRLs between late and early summer (before and after July 15). In decline years 1967 and for females in 1964 the mean length was increasing through the summer (Kendalls rank correlation coefficient = 2.735, $P < 0.01$ and 3.884, $P < .001$, respectively). Also in 1967 the mean SRL was higher in late than in early summer (Table 1) (separate variance estimate t = 2.89, d.f. = 11.65, P = .014; SPSS/PC+, t-test groups; all t-tests have been made by the same procedure).

In 1964 the SRLs of females were significantly higher in late than in early summer (t = 2.72, d.f. = 137.33, P = .007) but smaller for males (t = 2.27, d.f. = 28.4, P = .031). Males had significantly higher SRLs than females in early summer (t = 3.34, d.f. 26.76, P = .002) but not in late summer (t = .54, d.f. = 126.09, P = .591). This kind of difference between sexes did not exist in other years. This could be understood on the basis of differential

regulation of the sexes (VIITALA 1977). There exists much less space for males that have large home ranges when high ranking mature males are ousting all the younger competitors (c.f. KALELA 1971). In high density situations dispersal may be almost the same as mortality (TAMARIN 1977). The young females are not ousted but they just do not attain maturity in their season of birth (KALELA 1957; VIITALA 1977). Because of the high density attained in late summer 1963 the males may have been sorted by rank already at that occasion with only postbreeding males of equal rank being left. During the decline in the following summer other factors may have become important. I suggest that during a decline, rank is the first factor improving survival. If all animals are equally ranking then young animals may be favoured (c.f. VIITALA 1977). In optimal situation there did not exist other differences in survival of different age groups except those in males during high density.

During severe summer decline in 1970 the SRL was increasing from May to July (means 1.505, 1.652 and 1.811, respectively). Because of the rapid decline (VIITALA 1977) only 8 animals were captured in mouse traps after the end of June. The difference between June and July samples was not significant (t = 1.55, d.f. = 8.91, P = .157) but the May value was significantly smaller than those of June and July (t = 2.24, d.f. = 19, P = .037 and t = 2.74, d.f. = 11.5, P = .018, respectively) (Table 1). The better survival of the oldest animals during that summer was demonstrated by live trapping data, too (VIITALA 1977).

The different development of age structure in males and females during the early decline in summer 1964 was associated by habitat preferences, too. The males were captured significantly more often on barren ground than were females (chi square = 7.606, d.f. = 1, p = .005). Data for such examination were available for peak summer 1969, too. The distribution of the sexes was the same (chi square = .0004, d.f. = 1, p = .979) in the case. The difference between years 1964 and 1969 was also in interspecific competition which was more severe in the latter year (VIITALA 1977). Also 1964 was a decline year but 1969 a peak year. The *Clethrionomys* males seem to be subordinate to females (MIHOK 1976; VIITALA 1977). Thus, the females may have been ousting males from eutrophic habitats to barren ground during the decline 1964.

After the beginning of the decline in 1964 the females had significantly higher mean SRL i.e. were older in oligotrophic heath forests than in eutrophic meadow forests (Table 1). Thus, the decline may have began in these barren habitats. The SRL of females in meadow

Table 1. **Mean SRLs of molars in *C. rufocanus* in eutrophic and oligotrophic habitats in 1964 and 1969 i. e. years when data are available**

Time	1964Jn		1964mJn		1964fJA		1964mJA		1969f		1969m	
habitat	eutr.	oligotr.	eutr.	oligotr.	eutr.	oligotr.	eutr.	oligotr.	eutr.	oligotr.	eutr.	oligotr.
mean	1.6072	1.5776	1.7720	1.7590	1.5608	1.6896	1.5725	1.6325	1.8289	1.5680	1.7100	1.8412
s. dev.	.183	.263	.437	.266	.241	.246	.196	.269	.245	.171	.294	.290
s. err.	.044	.062	.195	.067	.049	.037	.057	.039	.082	.111	.038	.057
N	18	17	5	16	24	45	12	48	9	7	7	26
t/P	.39/.701		.06/.954		2.08/.041*		.87/.391		2.89/0.014*		1.06/.319	

Explanations as in Table 1 except Jn = June, JA = July and August, t/P = Students t-test score/probability, * = significant

Table 2. **The mean SRLs of second upper molar of *C. rufocanus* in June samples in different years and ways of trapping**

Year	1964fo	1964mo	1965o	1967o	1968o	1968L	1969o	1969L	1970o	1970L	totals
mean	1.5288	1.7368	1.5455	1.6823	1.8685	1.9056	1.6924	1.8377	1.6337	1.8514	1.694
N	34	56	11	13	20	18	49	30	88	21	340
s. dev.	.354	.246	.203	.355	.186	.273	.335	.278	.299	.270	.312
s. err.	.061	.033	.061	.099	.042	.064	.048	.051	.032	.059	.017

Explanations: o = catches on optimal habitats made with small mouse snap traps; L = samples in suboptimal lemming habitats made with bigger rat traps; N = sample size; s. dev and s. err. = standard deviation and standard error, f = females and m = males. Columns without either sign = both sexes combined

woods in late summer 1964 did not deviate from that in early summer. Thus the decline had not yet begun there! This may be related to the finding of Oksanen and Oksanen (1981) that the dwarf shrubs of oligotrophic habitats formed antiherbivory phenols during high browsing pressure but the herbs and grasses dominating eutrophic meadow woods did not. Thus, it is suggested that food may have been the main reason of the beginning of decline in that particular case.

In the severe interspecific interaction during summer 1969 the mean SRL of females was higher in eutrophic than in oligotrophic woods (Table 1). This was caused by the intrusion of *Microtus agrestis* on meadow woods. Only the high ranking old animals could resist them, others were ousted (Viitala 1977). Field voles are unable to occupy heath forests, however (Kalela et al. 1971). Thus the age structure of *C. rufocanus* remained unchanged there (c.f. Viitala 1977).

Mean ages in optimal vs. suboptimal habitats

There was a statistically highly significant difference between the mean SRLs in samples collected in optimal habitats with baited mouse traps and those collected in suboptimal lemming habitats with unbaited rat traps in 1968–1970 indicating higher mean age in suboptimal habitats (t = 6.11, d.f. 129.59, 2-tail P = 0.000) (Table 2). The same was true for yearly samples 1969 and 1970 (t = 2.08, d.f. 70, p = .041 and t = 3.24, d.f. 32.86, P = .003, respectively). There is some doubt, however, that this difference is at least partly caused by trapping method since in simultaneous trappings in July 1969 in EMT-*(Empetrum-Myrtillus)* heath wood the mean age was higher in animals captured with unbaited rat traps than in those captured with baited mouse traps! (t = 2.11, d.f. 34.99, P = .042, N = 16/21). However, the reason may be that the lemming habitats were moss dominated but the mouse trappings were done in dwarf scrub covered heath woods. This view was supported in June 1968 after a decline when the mean SRL was the same both in lemming and mouse trappings (t = .17, d.f. 44.86, p = .867) and even in optimal habitats was significantly higher than in other years in optimal habitats (t = 5.09, d.f. 28.14, P = .000, N = 251/20). The small sample obtained after decline in June 1965 did not deviate from other years in optimal habitats, however. This may have been caused by anomalies in tooth growth or by accident due to small sample size.

Conclusions

Zejda (1961) first observed the better survival of oldest *C. glareolus* during winter decline. The M^2-method without

calculating the mean SRL may not allow careful examination of survival of overwintered cohorts. Thus in all previous studies the overwintered animals are grouped in one cohort.

I conclude that high age may be an advantage in stressful environment and phases of cycle. I believe the most likely reason is social the high ranking animals being able to quarantee sufficient resources even in a deteriorating environment. There seem to be differences in the social status among old breeding animals, even among territorial females. The differences among mature males have previously been discussed e.g. by VIITALA (1977), GUSTAFSSON et al. (1980), and HOFFMEYER (1982, 1983).

Social dominance may be an important demographic factor in any circumstances causing increased mortality. It has been shown that most reproducing animals do not die during winter, but several of them continue to reproduce in their second summer in the subarctic Kilpisjärvi region. In most years this age group is of little importance but after the decline it seems to be the fraction that leads the population to a new increasing phase (VIITALA 1977).

In *Clethrionomys* the changes in mean SRL can be used as a sensitive indicator of changes in mortality. It is much less laborius than the other method available i.e. extensive live trapping. Increasing mortality takes more the youngest overwintered animals thus favoring animals that have been reproducing already in their first summer. Their fates can not be estimated on the basis of any genital markers which disappear at last in the beginning of a new breeding season (VIITALA 1977).

I believe, that other age indicators than molar roots, also can be standardized in same way to study changes in age structure by time without to group the animals in separate cohorts.

Acknowledgements

I am greatly indepted to the late Prof. OLAVI KALELA for providing me most of the material of the present study. His stimulating enthusiasm and deep realism have greatly affected my thoughts. Prof. MICHAEL S. GAINES has kindly read the first draft of the manuscript and made valuable suggestions on it. The errors are my own, however. This study has been supported by grants by The Finnish Acamedy of Sciences, the State Board of Science and the Eemil Aaltonen foundation.

Zusammenfassung

Eine Methode zur Bestimmung von Unterschieden im Überleben von Graurötelmäusen (Clethrionomys rufocanus) in Kilpisjärvi, Finnisch Lappland

Die auf den 15. Juni bezogene, standardisierte Wurzellänge (SRL) am M^2 von Graurötelmäusen *(Clethrionomys rufocanus)* kann als Maß für das mittlere Alter Indikator für die Mortalität sein. Mit dieser Methode konnte die Überlebensrate im 2. Sommer zu verschiedenen Zeiten des Dichtezyklus, in unterschiedlichen Habitaten und zwischen den Geschlechtern verglichen werden. Dabei zeigte sich, daß während eines Populationsrückganges das mittlere Alter zunimmt, und daß dieses in oligotrophen Wäldern früher eintritt als in eutrophen. Männchen und Weibchen verhielten sich während des Populationsrückganges unterschiedlich.

Literature

GUSTAFSSON, T. O.; ANDERSON, C. B.; MEURLING, P. (1980): Effect of social rank on the growth of the preputial glands in male bank voles, *Clethrionomys glareolus.* Physiol. Behav. **24,** 689–692.

HENTTONEN, H.; VIITALA, J. (1982): *Clethrionomys rufocanus* (Sundevall 1846) – Graurötelmaus. In: Handbuch der Säugetiere Europas, Bd2/1, 147–164. Ed. by J. Niethammer and H. Krapp. Wiesbaden: akad. Verlagsges.

HOFFMEYER, I. (1982): Responses of female bank voles *(Clethrionomys glareolus)* to dominant vs. subordinate conspecific males and to urine odours from dominant vs. subordinate males. Behav. Neur. Biol. **36,** 178–188.

— (1983): Interspecific niche separation in wood mice (*Apodemus flavicollis* and *A. sylvaticus*) and scent marking relative to social dominance in bank voles *(Clethrionomys glareolus).* Ph. D. thesis. Department of Animal Ecology, University of Lund.

Kalela, O. (1957): Regulation of the reproduction rate in subarctic populations of the vole *Clethrionomys rufocanus* (Sund.). Ann. Acad. Sci. Fennicae (A IV) **34,** 1–60.
— (1971): Seasonal trends in the sex ratio of the grey sided vole, *Clethrionomys rufocanus* (Sund.). Ann. Zool. Fennici **8,** 42–455.
Kalela, O.; Koponen, T.; Yli-Pietilä, M. (1971): Übersicht über das Vorkommen von Kleinsäugern auf verschiedenen Wald- und Moortypen in Nordfinnland. Ann. Acad. Sci. Fennicae (A IV) **185** 1–13.
Koshkina, T. V. (1955): (A method for determination of the age of common red-backed voles and experience of its application.) Zool. Zhurn. **34,** 631–639. (In Russian).
Lowe, V. P. (1971): Root development of molar teeth in bank vole *(Clethrionomys glareolus).* J. Anim. Ecol. **40,** 49–61.
Oksanen, L.; Oksanen, T. (1981): Lemmings *(Lemmus lemmus)* and grey-sided voles *(Clethrionomys rufocanus)* in interaction with their resources and predators on Finnmarksvidda, northern Norway. Rep. Kevo Subarctic Res. Stat. **17,** 7–31.
Perrin, M. R. (1978): Molar root-length as an indicator of age in *Clethrionomys gapperi.* Acta Theriol. **23,** 423–434.
Tamarin, R. H. (1977): Dispersal in island and mainland voles. Ecology **58,** 1044–1054.
Tupikova, N. V.; Sidorova, G. A.; Konovalova, E. A. (1968): A method of age determination in *Clethrionomys.* Acta Theriol. **13,** 99–115.
Viitala, J. (1971): Age determination in *Clethrionomys rufocanus* (Sundevall). Ann. Zool. Fennici **8,** 63–67.
— (1977): Social organization in cyclic subarctic populations of the voles *Clethrionomys rufocanus* (Sund.) and *Microtus agrestis* (L.). Ann. Zool. Fennici **14,** 53–93.
— (1980): (Sociology of *Microtus* and *Clethrionomys* in Kilpisjärvi). Luonnon Tutkija **84,** 31–34. (In Finnish, with English summary).
— (1984): The red vole, *Clethrionomys rutilus* (Pall.), as a subordinate member of the rodent community at Kilpisjärvi, Finnish Lapland. Acta Zool. Fennica **172,** 67–70.
Viro, P. (1974): Age determination in the bank vole, *Clethrionomys glareolus* Schreb. 1780, from roots of the teeth. Aquilo Ser. Zool. **15,** 33–36.
Wiger, R. (1979): Demography of a cyclic population of the bank vole, *Clethrionomys glareolus.* Oikos **33,** 373–385.
Zejda, J. (1961): Age structure in populations of bank vole *Clethrionomys glareolus* Schreber, 1780. Zool. Listy **10,** 249–264.

Author's address: Jussi A. Viitala, Konnevesi Research Station, University of Jyväskylä, SF–44300 Konnevesi, Finland

Z. Säugetierkunde 54 (1989) 229–238

ISSN 0044-3468

Tagesrhythmik der motorischen Aktivität bei der Mongolischen Rennmaus *(Meriones unguiculatus)*

Von Th. Heinzeller und B. Aschauer

Aus der Anatomischen Anstalt (Lehrstuhl III) der Universität München

Eingang des Ms. 9. 11. 1987

Abstract

Daily patterns of motor activity in the Mongolian gerbil

Studied the motor activity of adult males of *Meriones unguiculatus* under different lighting conditions. Although interindividual as well as day to day variability is high, in all a circadian rhythm exists which runs free in LL. The shape of the daily activity distribution primarily is biphasic, the main summit (acrophase of the 24 h-component) occurring in the late afternoon. Short day conditions make the animals merely nocturnal, indicated by high average activity at night including a shift of maximal activity towards midnight. Under long day conditions, the animals prefer light time activity with peaks at dawn and dusk. This last-mentioned peak shifts toward darkness with increasing light-intensity.

Einleitung

Die Mongolische Rennmaus findet wegen einer Reihe günstiger Eigenschaften in zunehmendem Maße Eingang in experimentell arbeitende Labors. Viele anatomische, physiologische und verhaltensbiologische Charakteristika dieser Spezies wurden von Thiessen und Yahr (1977) zusammengetragen. Doch zur Frage einer Tagesperiodizität in der Aktivität dieser Tiere fehlen verläßliche Angaben sowohl in der von Thiessen und Yahr gesichteten Literatur wie auch in weiteren Untersuchungen, die teils unter seminatürlichen Bedingungen, teils bei üblicher Käfighaltung durchgeführt wurden. Die Ergebnisse verschiedener Autoren sind so wenig einheitlich wie der Eindruck, den man bei Stallbesuchen gewinnen kann: wenn die Tier- und Käfigzahl nicht zu klein ist, trifft man zu jeder Zeit des Tages und der Nacht sowohl muntere Tiere wie auch Schlafkugeln an. Entsprechend wird *Meriones unguiculatus* als nachtaktiv (Thiessen et al. 1968), als sowohl tag- wie auch nachtaktiv (Tanimoto 1943; Bannikov 1954) oder auch als tagaktiv (Roper und Polioudakis 1977) beschrieben. Dabei soll die Aktivitätsverteilung je nach Autor unimodal oder auch bimodal aussehen. Sicher beruhen diese Differenzen zum Teil darauf, daß zu kleine Tierzahlen beobachtet wurden, aber auch ein Einfluß der unterschiedlichen Haltungsbedingungen kann nicht ausgeschlossen werden. Deshalb haben wir das Aktivitätsmuster an einem größeren Untersuchungsgut bestimmt und versucht, dieses Muster durch Variation von zwei Umweltparametern zu modifizieren.

Material und Methode

Tiere. Insgesamt wurden 50 adulte männliche Tiere von *Meriones unguiculatus* untersucht. Sie stammten aus eigener Zucht, blieben bis zum Alter von 50 Tagen mit den Wurfgeschwistern bei der Mutter, dann mit den Wurf-Brüdern zusammen, bis sie 120 Tage alt waren, und wurden dann isoliert gehalten. Altruminpellets und Wasser standen ad libitum zur Verfügung. Das Tierzimmer war fensterlos, die Raumtemperatur wurde bei 20 °C konstant gehalten. Alle Käfige standen auf Tischen nebeneinander unter der Deckenbeleuchtung, die Beleuchtungsstärke betrug (in allen Käfigen) 40 Lux. Sollte ein Tier stärker beleuchtet werden, wurde sein Käfig durch einen Vorhang von den anderen abgetrennt und eine zusätzliche Lampe bzw. ein Halogenscheinwerfer aufgestellt.

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5404-0229 $ 02.50/0

Registrierung. Uns stand ein Animex-Gerät zur Verfügung (Farad-Electronics, Schweden), das die Störung eines elektromagnetischen Feldes durch sich bewegende Tiere impulsweise registriert (maximal 5 Impulse/sec), summiert und stündlich ausdruckt. Unsere Werte repräsentieren also Bewegungen aller Art, soweit sie nur mit einer Mindestbeschleunigung eines Tierkörpers einhergehen, d.h. Aktivitäten der Nahrungsaufnahme ebenso wie Laufen, Graben etc.

Versuche. Diese Gesamtaktivität wurde registriert

a. von einer Gruppe von 3 friedlich koexistierenden Rennmäusen, und zwar 15 Tage unter LD 16:8 und 20 Tage unter Dauerlicht,
b. von 27 Einzeltieren under LD 14:10, jeweils für 3 Tage,
c. von 10 Einzeltieren, die an LD 14:10 adaptiert waren, nach Umstellung auf LD 8:16 (mindestens 24 Tage Anpassung) für je 3 Tage sowie nach erneuter Umstellung auf LD 16:8 (mindestens 24 Tage Anpassung) für nochmal 3 Tage. Je ein Tier dieser Gruppe wurde während beider Anpassungsphasen durchgehend registriert,
d. von 10 Einzeltieren, die im LD 14:10 aufgewachsen waren, jeweils für 3 Tage bei 40 Lux, 3 Tage bei 400 Lux und 3 Tage bei 4000 Lux (im Käfig).

Auswertung. Die Werte aus Versuch a. wurden einer Spektralanalyse unterworfen (mit dankenswerter Hilfe durch Dr. L. v. Lindern, Leiter des Rechenzentrums am Klinischen Institut des Max-Planck-Institutes für Psychiatrie München). Die Spektralanalyse filtert aus einer Zeitreihe periodisch wieder-

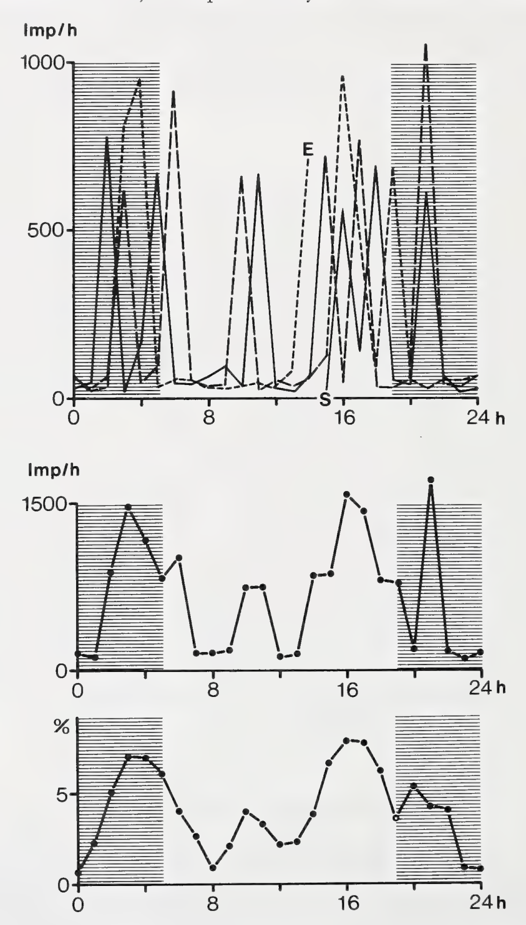


Abb. 1. Beispiele für die Registrierung eines Individuums. Oben: stündliche Impulswerte von 3 fortlaufenden Tagen, beginnend bei S, endend bei E. Mitte: Impulssumme dieser 3 Tage. Unten: Impulssumme in % der insgesamt registrierten Aktivität nach Glättung. Dunkelzeiten sind querschraffiert

kehrende Ereignisse heraus und erlaubt eine Aussage darüber, welche Frequenzen überzufällig stark in der Zeitreihe vertreten sind. So kann z. B. geklärt werden, ob in einer solchen längerfristigen Registrierung von Ereignissen eine Tagesperiodik enthalten ist oder nicht, und wenn ja, mit welcher Deutlichkeit (Konfidenz)., Werte aus b., c. und d. wurden (vgl. Abb. 1) zunächst bei jedem Individuum über 3 Tage summiert, durch gleitende Mittelwertbildung geglättet und schließlich auf die gesamte Impulssumme dieses Tieres normiert. Erst dann wurde über alle an einem Versuch beteiligten Tiere gemittelt.

Ergebnisse

Versuch a: Folgt die Aktivitätsverteilung einem Rhythmus?

Die Mitglieder einer Gruppe sind erfahrungsgemäß weitgehend synchron aktiv. Deshalb konnte der erste Versuch mit 3 friedlich koexistierenden Männchen durchgeführt werden. Die 15tägige Abfolge der registrierten Impulse ist in Abb. 2 (oben) wiedergegeben. Auf den ersten Blick ist keinerlei auffällige Rhythmik zu erkennen. Werden indes diese Werte einer Spektralanalyse unterworfen, dann tritt eine rhythmische Komponente der Periodenlänge 24 h zutage. Die Abb. 2 zeigt rechts unten eine sog. Cosinor-Graphik, d.i. eine „Tagesuhr" (6 Uhr rechts, 12 Uhr unten etc.), in der die Dunkelzeit als punktierter Sektor ausgewiesen ist. Die Pfeile (ähnlich Uhrzeigern) weisen auf die Phase der 24-h-Komponente bei 18.15 Uhr bzw. auf die Phasen der 12-h-Komponente kurz nach 7 und kurz nach

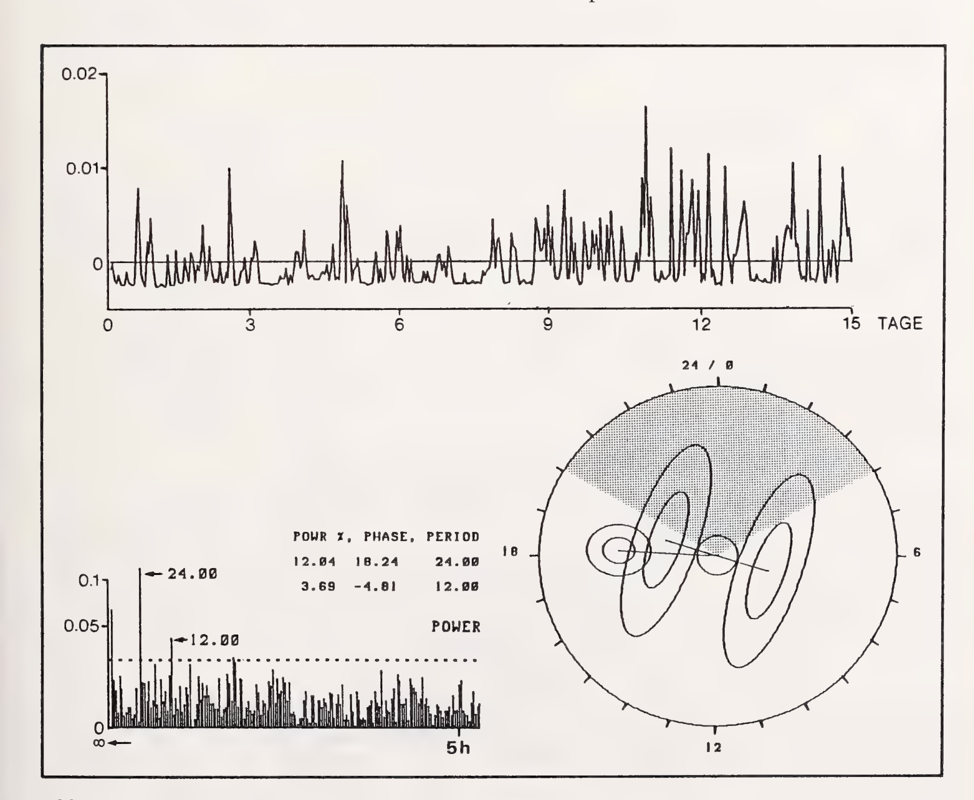


Abb. 2. Frequenzanalyse einer Gruppenregistrierung über 15 Tage. Oben: Aktivitätswerte relativ zum Gesamtdurchschnitt. Unten rechts: Hauptergebnis der Frequenzanalyse in Cosinor-Darstellung; Dunkelzeit punktiert. Unten links: Power-Spektrum, die gepunktete Linie entspricht dem 4fachen des Grundrauschens, deutlich ragen darüber die Besetzungswerte der 12- und der 24-h-Komponente sowie (ganz links) eines langfristigen Trends hinaus

19 Uhr. Die beiden Ellipsen an den Zeigerenden symbolisieren das Bestimmtheitsmaß (Konfidenz). Je höher die Konfidenz, desto kleiner sind die Ellipsen: bei der 24-h-Komponente beträgt die Konfidenz 99 %, bei der 12-h-Periodizität 95 %. Die Konfidenz wird aus der relativen Besetzung („Power") der jeweiligen Frequenz berechnet. In Abb. 2 ist links unten zu 109 überprüften Frequenzen (der Wert Null entspricht einer unendlich langen Periode, das rechte Abszissenende einer Periode von 267 min) die zugehörige Besetzung aufgetragen. Man sieht, daß die gepunktete Linie, die dem 4fachen Grundrauschen entspricht, von der 24-h- und der 12-h-Komponente deutlich überschritten wird. Dieses erste Ergebnis belegt die Existenz eines Aktivitätsrhythmus bei *Meriones unguiculatus*, in dem die 24-h-Periode vorherrscht. Ein entsprechender Versuch mit 3 weiblichen Tieren führte zu einem sehr ähnlichen Ergebnis: mit jeweils 99 %iger Konfidenz konnte eine 24-h-Periode mit Phase bei 18.22 Uhr und eine 12-h-Periode mit Phasen bei 6.20 bzw. 18.20 festgestellt werden.

Ob sich in diesen Periodizitäten ein endogener circadianer Rhythmus ausdrückt oder ob lediglich externe Zeitgeber abgebildet werden, wurde durch einen Versuch im Dauerlicht geprüft. Abbildung 3 zeigt die Aktivitätsverteilung der vorigen Tiere im LL: offensichtlich läuft der Rhythmus frei. Das wurde dadurch sichtbar gemacht, daß in der Zeichnung nur die Aktivitätsspitzen repräsentiert wurden. Die Periodenlänge wird zu 26½ h berechnet, Konfidenz 99 %. Auch dieses Experiment wurde mit einer Weibchengruppe bestätigt (Periodenlänge 24 h, Konfidenz 99 %). Im Dauerlicht gibt sich der Rhythmus durch seinen freien Lauf als endogen, durch die Periodenlänge als circadian zu erkennen.

Versuch b: Wie sieht die circadiane Aktivitätsrhythmik aus?

Trotz inter-individueller Schwankungen, die sich in der Standardabweichung der Durchschnittskurve ausdrücken, zeigt Abb. 4 als Tenor der Aktivitätsverteilung ein bimodales Muster mit mitternächtlichem Minimum. Ein schwach ausgeprägter Buckel der Aktivitätsverteilung wird am Vormittag beobachtet, das Hauptmaximum liegt bei 18.15 Uhr. Werden die Werte in ein Blockdiagramm übertragen (Abb. 4, rechts), in dem die Blockhöhe die durchschnittliche Aktivität während der Dunkel-, der Hellzeit und während zweier um die Beleuchtungswechsel gelegener 4-h-Bereiche bedeutet, die Fläche der Blöcke also ein Maß für die Gesamtaktivität in einer bestimmten Zeitspanne darstellt, dann geben sich die Tiere – wie schon zuvor durch die Lage der Aktivitätsmaxima – als eindeutig

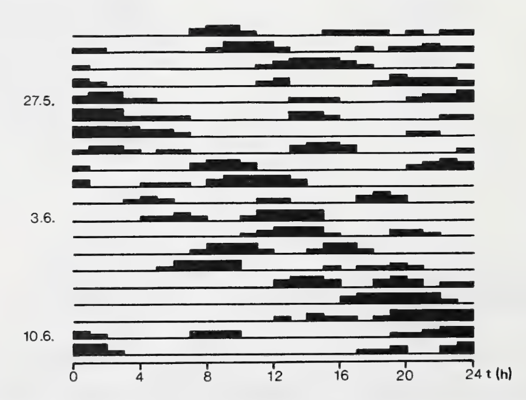


Abb. 3. Gruppenregistrierung im Dauerlicht. Dargestellt sind nur die Aktivitätsspitzen: die 3 Stufen der schwarzen Balken entsprechen Aktivitätswerten von bis 150 %, bis 200 % und mehr als 200 % der durchschnittlichen Aktivität (Grundlinie). Das Hauptmaximum der Aktivität wandert mit einer Periodenlänge von 26 h 31 min nach rechts

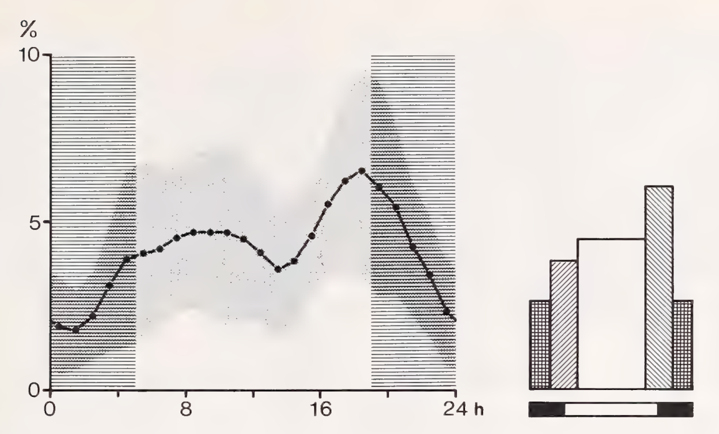


Abb. 4. Aktivitätsverteilung im Langtag, 27 Tiere. Links: Mittelwert und Standardabweichung (punktierter Bereich). Rechts: Blockdiagramm der Aktivität in der Nacht (doppelt schraffiert), in der reinen Hellzeit und in 2 jeweils 4 h breiten „Dämmerungszeiten", die zur Hälfte vor und zur Hälfte nach dem Lichtwechsel liegen (schräg schraffiert)

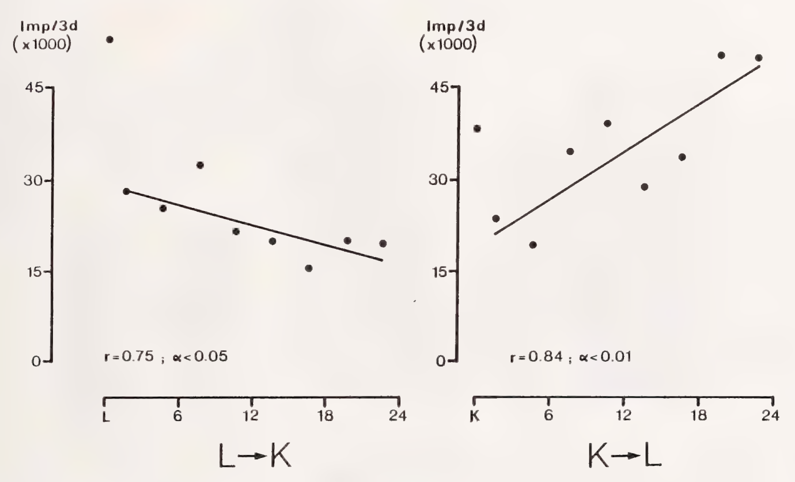


Abb. 5. Umstellung der Gesamtaktivität auf niedrigere Werte beim Übergang vom Lang- in den Kurztag (L→K) bzw. auf höhere Werte beim Übergang vom Kurz- in den Langtag (K→L). Aufgetragen sind jeweils 3tägige Impulssummen, verfolgt wurde die Umstellung an je einem Individuum über 24 Tage. Die Regressionsberechnungen beruhen auf Kurztagbeobachtungen (links) bzw. Langtagbeobachtungen (rechts); doch wurde zum Vergleich über den Nullpunkt der Zeitachse die vorausgegangene Langtag-Aktivität bei L bzw. die vorausgegangene Kurztag-Aktivität bei K eingezeichnet

tagaktiv zu erkennen mit einer zusätzlichen Bevorzugung der Zeit der Abenddämmerung. Das gilt für die hier gewählten Bedingungen: Langtag 14:10 und 40 Lux Beleuchtungsstärke.

Versuch c: Wie wirkt sich eine Änderung der Tageslänge aus?

Während der Eingewöhnung der Gruppe in die Kurztagverhältnisse wurde exemplarisch an einem Individuum der Umstellungsvorgang 24 Tage lang verfolgt (Abb. 5, links). Die Gesamtaktivität geht erheblich zurück. Ein anderes Individuum, an dem die Übergangs-

funktionen für den Wechsel vom Kurz- in den Langtag mitgeschrieben wurden, zeigt einen Anstieg der Gesamtaktivität (Abb. 5, rechts).

Wie bei diesen beiden Einzeltieren tritt auch im Gesamtdurchschnitt von 10 untersuchten Tieren eine höhere Dunkelaktivität im Kurztag bzw. eine höhere Hellaktivität im Langtag auf, was aus den Blockdiagrammen der Abb. 6 entnommen werden kann. Die Verteilungskurve selbst behält ihren zweigipfeligen Verlauf, doch ist im Kurztag das Hauptmaximum weit in die Nachtzeit hineinverschoben und umfaßt sogar noch Mitternacht, im Langtag rückt es wieder um 2½ h vor. Hellaktive Langtagtiere werden also im Kurztag dunkelaktiv und vice versa.

Im Vergleich zum Hauptmaximum treten beim Nebenmaximum während der vorgegebenen Eingewöhnungszeit keine Verschiebungen auf.

Versuch d: Welchen Einfluß hat die Beleuchtungsstärke?

Eine Gruppe von Tieren, die im Langtag aufgewachsen waren, wurde bei der stallüblichen Beleuchtungsstärke von 40 Lux registriert (Abb. 7, oben) sowie bei 400 bzw. 4000 Lux. Je hellerem Licht die Tiere ausgesetzt waren, desto weiter verschiebt sich das abendliche

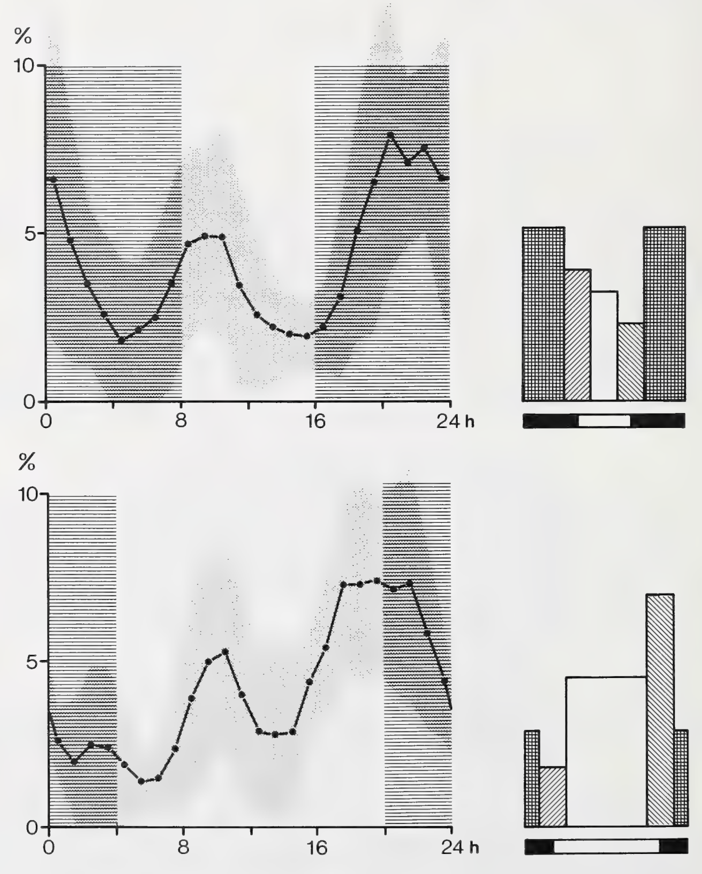


Abb. 6. Aktivitätsverteilung im Kurztag (oben) und extremen Langtag (unten), 10 Tiere. Blockdiagramme rechts entsprechend Abb. 4

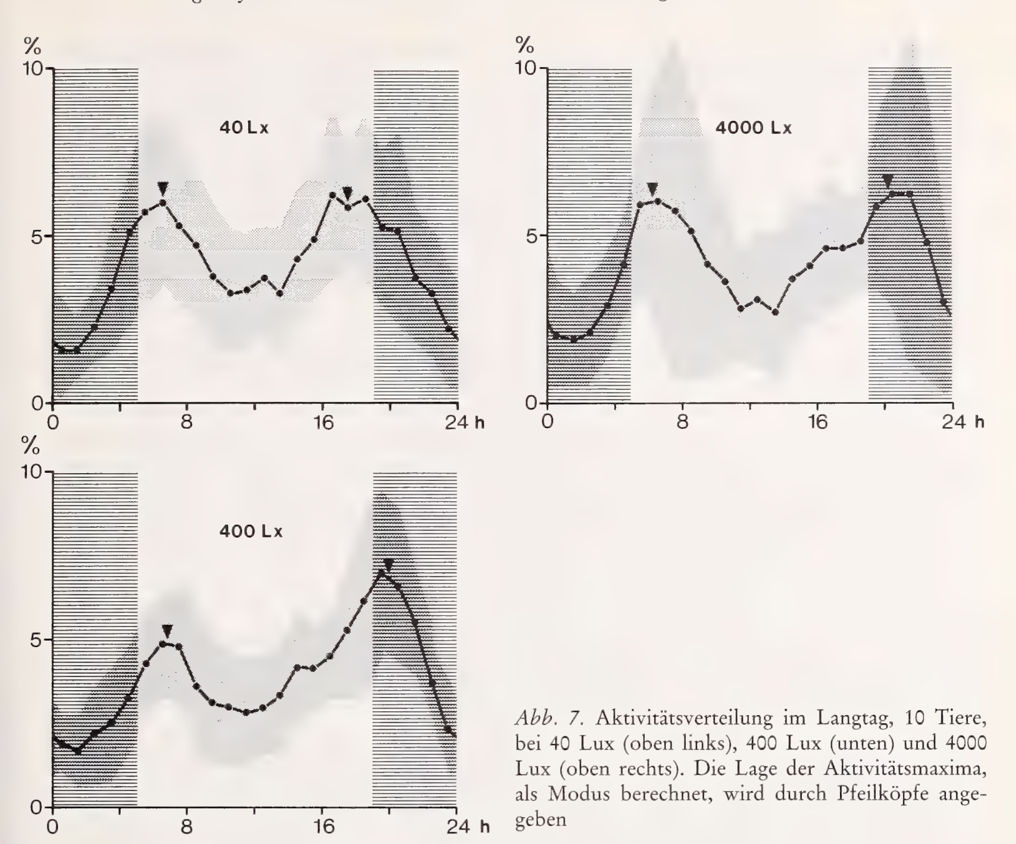


Abb. 7. Aktivitätsverteilung im Langtag, 10 Tiere, bei 40 Lux (oben links), 400 Lux (unten) und 4000 Lux (oben rechts). Die Lage der Aktivitätsmaxima, als Modus berechnet, wird durch Pfeilköpfe angegeben

Maximum in die Dunkelzeit hinein, bei unserem Untersuchungsgut immerhin um mehr als 2 h (Pfeilköpfe in Abb. 7). Hier bahnt sich also ein Übergang von der Tag- zur Nachtaktivität an, womit sich die Tiere als dämmerungsaktiv erweisen.

Diskussion

In wesentlichen Punkten stimmen unsere Befunde mit denen von Stutz (1972) und Pietrewicz et al. (1982) überein, sie weichen ab von Thiessen et al. (1968), von Lerwill (1974), von Roper (1976) und von Roper and Polioudakis (1977). Zum Teil können die Widersprüche daraus erklärt werden, daß die interindividuelle Schwankung, die auch in unserem Untersuchungsgut stark bemerkbar ist, bei Verwendung zu kleiner Tierzahlen noch nicht kompensiert wird. Zum Teil beruhen sie sicher auch auf der Verwendung unscharfer Termini und/oder auf methodischen Differenzen.

Die Begriffe „Tag-", „Nacht-" und „Dämmerungsaktivität" stammen aus der Praxis der Tierbeobachtung; sie sind unverzichtbar, doch ungenau: Was heißt aktiv? Wenn wir der Definition von Aschoff (1962) folgen, ist „ein Tier . . . tätig, wenn es Körperteile bewegt oder sich selbst fortbewegt". Damit wird der träumende Hund, die zum Wiederkäuen gelagerte Kuh ebenso eingeschlossen wie die stereotypen Läufe des Gepards im Zoo. Dennoch bleibt ein so umfassender Begriff von Aktivität aus pragmatischen Gründen wertvoll, zumal sich die Häufigkeitsverteilung einzelner Verhaltensweisen oft mit der der Gesamtaktivität weitgehend deckt, wie das bei *Meriones unguiculatus* für Lokomotion,

Graben, Autogrooming, Essen (Ausnahme: Trinken) gezeigt wurde (Pietrewicz et al. 1982). Weit problematischer ist die Zuordnung eines Aktivitätsmusters zu Tageszeiten: Ist die Lage des Aktivitätsgipfels entscheidend? Dann müßten unsere Langtagtiere bei 40 Lux als tag-, bei 4000 Lux als nachtaktiv bezeichnet werden. Vielleicht sollte man eher die Aktivitätssumme eines Tagesabschnittes entscheiden lassen. Aber auch wenn der Vorteil einer solchen Betrachtung durch die Blockdiagramme der Abbildungen 4 und 6 demonstriert wird, sollte ergänzend Zahl und Lage der Maxima genannt werden. Zusätzlich müssen ausreichende Angaben über die Haltungsbedingungen während der Untersuchung gemacht werden, denn Aktivitätsmuster erweisen sich gerade durch ihre Varianz (zwischen Arten, zwischen Habitaten, zwischen Individuen) als Ergebnis der Auseinandersetzung mit der Umwelt.

Bei Säugetieren sind sehr unterschiedliche Abfolgen von Aktivitäts- und -ruhezeiten verwirklicht. Neben Arten, bei denen eine circadiane Organisation nur schwer zu erkennen, weil durch zahlreiche infradiane Kurzperioden überdeckt ist (z. B. Hausspitzmaus, Genoud und Vogel 1981), reicht die Skala von ganz strikter Nachtaktivität (z. B. Gleitbeutler, Kleinknecht et al. 1985) und weitgehender Nachtaktivität mit kleinen Ausnahmen in der Hellzeit (z. B. Europäischer Igel, Boitani and Reggiani 1984) über Formen mit lediglich einer Bevorzugung der Dunkelheit (z. B. Meerschweinchen, Büttner und Wollnik 1982) bis hin zu exklusiver Tagaktivität (z. B. Spitzhörnchen, Weigold 1979); die Skala schließt auch viele Formen ein, die vor allem in den Dämmerungszeiten aktiv sind, wie etwa der Alpensteinbock (Böck 1984), und die damit zum „Bigeminustyp“ der Aktivitätsverteilung nach Aschoff (1957) überleiten. Dieser Typ ist durch Maxima zu Beginn und gegen Ende der Aktivitätszeit gekennzeichnet und wird unter den dunkelaktiven Formen z. B. durch das Meerschweinchen vertreten. Bei den hellaktiven Formen kann *Meriones unguiculatus* als Repräsentant gelten.

Auch wenn die Aktivitätsverteilung einer Spezies einem ererbten Grundmuster folgt, ist sie nicht einfach als Invariable zu sehen sondern im Rahmen ökologischer Anpassung. So können in dieser Hinsicht auch zwischen einander nahe stehenden Arten beträchtliche Unterschiede festgestellt werden, wie etwa für einige Arten der Gattungen *Gerbillus* und *Meriones* (Fiedler 1972). Dabei ist zu erwarten, daß die Aktivitätsrhythmik nicht starr das Habitat abbildet, sondern dessen Veränderungen adäquat beantworten kann. Das Verbreitungsgebiet von *Meriones unguiculatus* erstreckt sich in nord-südlicher Richtung von Korea bis in die Mongolei; damit sind verschiedene Populationen dieser Art weniger starken bis extremen jahreszeitlichen Wechseln ausgesetzt. Eine circannuale Variation der Aktivität wurde 1977 von Natalini beobachtet. Auch der Einfluß, den eine Änderung des Erdmagnetfeldes auf die Spontanaktivität von *Meriones unguiculatus* ausübt (Stutz 1971), ist in diesen Zusammenhang zu stellen. Die Wechsel des Aktivitätsmusters bei Lang-, dann Kurz-, dann Langtaghaltung, wie sie hier berichtet werden, können ebenfalls als saisonale Anpassung aufgefaßt werden. Darüber hinaus könnte auch eine Korrelation gesehen werden zwischen der Lage der Maxima im hier beschriebenen Langtag-Bigeminus und der um die jeweils selbe Zeit von Leontjev (1954) im Freiland beobachteten hohen Zahl von Samen eintragenden Tieren; man könnte die bei den unter 4000 Lux gehaltenen Tieren besonders ausgeprägte mittägliche Siesta dahingehend interpretieren, daß sie an besonders hellen Tagen die Mittagshitze meiden. Man könnte sogar die Phase nächtlicher Aktivität bei den Kurztag-(„Winter-“)Tieren als thermoregulatorische Maßnahme verstehen (McFarland 1981). Solche Parallelen sollten indes trotz einer gewissen Plausibilität höchst vorsichtig gezogen werden; zum einen liegen keine ausreichenden Beobachtungen aus dem Freiland vor, zum anderen kann schon allein die Gefangenschaft mit allen Umständen der Haltung unter künstlichen Bedingungen (z. B. fehlt in den meisten Tierräumen eine Dämmerungsanlage) das Aktivitätsmuster stark beeinflussen oder nachgerade umdrehen, wie beim Kaninchen (Kraft 1978) und bei der Hausspitzmaus (Genoud and Vogel 1981) deutlich demonstriert wurde. Dabei verweisen die Letztgenannten ganz

zu Recht auf die besondere Bedeutung der Nahrungssuche für die Ausgestaltung circadianer und circannualer Rhythmen.

Mit der Wirkung von Außenparametern (Licht, Temperatur, Nahrung) interferiert die des spezies- und individualtypischen Verhaltens. Die hier untersuchte Art hat ein insgesamt stark ausgeprägtes exploratorisches Verhalten (Osborne 1977). Vermutlich geht davon auch unter den reizarmen Käfigbedingungen ein erheblicher Beitrag zur Spontanaktivität aus. Der starken interindividuellen Varianz dieses Verhaltens (Thompson and Lippman 1972) kann ein Teil der starken Streuung in den Mittelwertskurven zugeschrieben werden. Diese Streuung sollte aber weniger als Mangel denn als Charakteristikum bewertet werden, zumal darauf auch die Anpassungsfähigkeit von *Meriones unguiculatus* beruhen dürfte. Diese Spezies eignet sich vielleicht gerade wegen ihrer Plastizität besonders für eine Analyse der multifaktoriellen Entstehung von circadianen und circannualen Aktivitätsrhythmen.

Zusammenfassung

Adulte Männchen von *Meriones unguiculatus* haben einen nicht besonders prägnanten, aber noch deutlich nachweisbaren circadianen Aktivitätsrhythmus mit bimodalem Verlauf, dem im Langtag am ehesten das Etikett „dämmerungsaktiv" gerecht wird, im Kurztag sind die Tiere nacht- und morgenaktiv. Eine Modifikation dieser Aktivitätsverteilung ist auch durch die Beleuchtungsstärke zu erzielen.

Literatur

Aschoff, J. (1957): Aktivitätsmuster der Tagesperiodik. Naturwissenschaften **13**, 361–367.

— (1962): Spontane lokomotorische Aktivität. Handb. Zool. **8**, 11, 1–174.

Bannikov, A. G. (1954): Mammals of the Mongolian People's Republic. Trudy Mongol'skoi Komissii **53**, 410–415. Transl. D. Lay, distributed by Tumblebrook Farm, W. Brookfield, Mass., USA.

Böck, F. (1984): Beobachtungen zur Aktivitätsperiodik des Alpensteinbocks (*Capra ibex ibex* L.) im natürlichen Lebensraum. 58. Hauptversammlung Dt. Ges. f. Säugetierkunde, Göttingen.

Boitani, L.; Reggiani, G. (1984): Movements and activity patterns of hedgehogs *(Erinaceus europaeus)* in mediterranean coastal habitats. Z. Säugetierkunde **49**, 193–206.

Büttner, D.; Wollnik, F. (1982): Untersuchungen zur Kurzzeitperiodik beim Meerschweinchen (*Cavia aperea* f. porcellus). 1. Bewegungsaktivität unter Licht-Dunkel-Wechsel, Dauerdunkel und Dauerlicht. Z. Säugetierkunde **47**, 370–380.

Fiedler, U. (1972): Beobachtungen zur Biologie einiger Gerbillinen, insbesondere *Gerbillus (Dipodillus) dasyurus*, Myomorpha, Rodentia) in Gefangenschaft. II. Ökologie. Z. Säugetierkunde **39**, 24–41.

Genoud, M.; Vogel, P. (1981): The activity of *Crocidura russula* (Insectivora, Soricidae) in the field and in captivity. Z. Säugetierkunde **46**, 222–232.

Kleinknecht, S.; Erkert, H. G.; Nelson, J. E. (1985): Circadian and ultradian rhythms of activity and O_2-consumption in three nocturnal Marsupialian species: *Petaurus breviceps*, Phalangeridae; *Dasyuroides byrnei*, Dasyuridae; *Monodelphis domestica*, Didelphidae. Z. Säugetierkunde **50**, 321–329.

Kraft, R. (1978): Beobachtungen zur Tagesperiodik von Wild- und Hauskaninchen. Z. Säugetierkunde **43**, 155–166.

Leontjev, A. N. (1954): Zur Ökologie der Mongolischen Rennmaus (Titel und Artikel in russischer Sprache). Isw. Irkutzk. protiwotschumn. Inst. Sibiri i daln. Wost. T. **12**, 137–149.

Lerwill, C. J. (1974): Activity rhythms of Golden hamsters *(Mesocricetus auratus)* and Mongolian gerbils *(Meriones unguiculatus)* by direct observation. Proc. zool. Soc. London **174**, 520–523.

McFarland, D. (1981): The Oxford Companion to Animal Behaviour. Oxford: Oxford Univ. Press.

Natalini, J. J. (1977): Circannual activity in the mongolian gerbil, *Meriones unguiculatus*. Am. Soc. Zoology **17**, 898.

Osborne, G. L. (1977): Differences in locomotor activity between rats and gerbils in response to novelty. Behav. and Biology **19**, 548–553.

Pietrewicz, A. T. (1982): Activity rhythms in the mongolian gerbil under natural light conditions. Physiol. and Behav. **29**, 377–380.

Roper, T. J. (1976): Sex differences in circadian wheel running rhythms in the mongolian gerbil. Phyiol. and Behav. **17**, 549–551.

Roper, T. J.; Polioudakis, E. (1977): The behaviour of Mongolian Gerbils in a semi-natural environment, with special reference to ventral marking, dominance and sociability. Behaviour 61, 207–237.

Stutz, A. M. (1971): Effects of weak magnetic fields on gerbil spontaneous activity. Annals of the New York Acad. of Sci. 312–323.

— (1972): Diurnal rhythms of spontaneous activity in the mongolian gerbil. Physiol. Zool. **45,** 325–333.

Tanimoto, K. (1943): Ecological studies of plaque-carrying animals in Manchuria. Zool. Mag. (Tokyo) **55,** 111–127. Transl. N. Chida, distributed by Tumblebrook Farm, W. Brookfield, Mass., USA.

Thiessen, D. D.; Lindzey, G.; Blum, S. L.; Tucker, A.; Fried, H. C. (1968): Visual behaviour of the mongolian gerbil *(Meriones unguiculatus).* Psychon. Sci. **11,** 23–24.

Thiessen, D. D.; Yahr, P. (1977): The gerbil in behavioural investigations. Austin-London: University of Texas Press.

Thompson, R. W.; Lippman, L. G. (1972): Exploration and activity in the gerbil and rat. J. Comp. Physiol. Psychology **80,** 439–448.

Weigold, H. (1979): Körpertemperatur, Sauerstoffverbrauch und Herzfrequenz bei *Tupaia belangeri* Wagner, 1841 im Tagesverlauf. Z. Säugetierkunde **44,** 343–353.

Anschrift der Verfasser: Prof. Dr. Th. Heinzeller und B. Aschauer, Anatomische Anstalt der Universität München, Pettenkoferstr. 11, D-8000 München 2, BR Deutschland

Z. Säugetierkunde 54 (1989) 239–242

ISSN 0044-3468

Weight estimation of Spanish ibex, *Capra pyrenaica*, and Chamois, *Rupicapra rupicapra* (Mammalia, Bovidae)

By P. Fandos, C. R. Vigal and J. M. Fernandez-Lopez

Estación Biologica de Doñana, Sevilla and Unidad de Zoologia Aplicada, Alcala de Henares, Madrid

Receipt of Ms. 20. 11. 1987

Abstract

The relationships of body weight to horn length, chest girth and body length were analysed for Spanish ibex, *Capra pyrenaica* (Schinz, 1838), and Chamois, *Rupicapra rupicapra* (L., 1758). Different linear regressions were necessary for each population and for each sex. All relationships were statistically significant ($p < 0.01$). The best predictors of body weight were horn length for male Spanish ibex, body length for female Spanish ibex, and chest girth for both sexes in the chamois.

Introduction

In recent studies of ungulates (Geist 1966; Nievergelt 1966; Bunnell 1978; Clutton-Brock et al. 1980) great importance has been placed on the relationship between horn length and body size and its ecological, ethological, and evolutionary implications. However, for control or populations management purposes, the relationships between horn length and body weight is also valuable. Nevertheless, since reliable data on body weight is frequently absent in museum specimens or mounted trophies, other linear measurements related to body size, like horn length, have been studied in several ungulates by a large number of authors, among them Ross (1958), Blood and Lovaas (1966), McEwan and Wood (1966), Nievergelt (1966), Rideout and Worthen (1975), Hall Martin (1977), Gray and Simpson (1979), Bunnell (1980), Clutton-Brock et al. (1980), and Popp (1985).

Although difficulties occur when estimating weight from linear measurements (Rideout and Worthen 1975), and sometimes low correlations (Bunnell 1978), this paper shows that the relationships between body weight and various linear measurements can be used to predict body weight in two populations of Spanish ibex, *Capra pyrenaica* (Schinz, 1838) and one of Chamois *Rupicapra rupicapra* (L., 1757).

Material and methods

Ibex specimens (n = 169) came from the Sierra de Cazorla, Southeast of the Iberian peninsula, and also from the Sierra de Gredos, Central Mountain Range, two of the main places within the area of distribution of the species. The chamois specimens (n = 47) came from the Cantabrican Mountains, Northwest of the Iberian peninsula. In both species specimens were obtained for a broad study of their biology and ecology from shootings during 1980–1984. Attention was paid to obtain a representative sample of each population in terms of sex, age and seasonality.

The specimens were weighed on a platform scale with a precision of ± 0.1 kg. Horn length (Horn) was measured by using a cord which was applied closely to the convoluted surface of the horn from tip to base. This measurement provided a better estimator of horn length than the simple measurement of the shortest distance between the base of the horn and its tip. Body length (LCC) was measured from the extreme of the snout to the base of the tail using a metric tape. During this procedure the stretched-out neck was bent so that it lay on the same plane as the trunk. The chest girth (PTOR) was taken by placing the tape around the body behind the front legs. All measurements were made in millimeters with a precision of ± 1 mm.

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5404-0239 $ 02.50/0

Using the body weight as a dependent variable and the linear measurements as independents, straight line regressions were treated separately owing to previously encountered significant differences (FANDOS and VIGAL in press).

Results

Horn length provided the most precise estimate of body weight in male ibex specimens from Gredos and from Cazorla ($R^2 = 0.86$ and 0.81 respectively, Table 1), while in females, this occurred with body length (LCC) ($R^2 = 0.82$ and 0.86). Error of estimation (Sxy) in these regressions were among the lowest ones. The chest girth measurement satisfactorily predicted body weight in both cases (see Table).

Regression equations used for the chamois gave different results. The highest value of R^2 was found between body weight and chest girth measurement (PTOR) ($R^2 = 0.86$ for males and 0.68 for females), while the lowest one was found between body weight and horn length. Although sexual dimorphism in the latter is not so pronounced as in the ibex, females showed a greater variability than males. All the regressions conform significantly to a probability lower than 0.01 (Table).

Discussion

In this paper males and females have been treated separately because of the significant sexual dimorphism occurring in both species (more pronounced in the ibex), the female/male rate in ibex is 0.35 for body weight and 0.15 for horn length (FANDOS 1986; FERNANDEZ-LOPEZ and GARCIA GONZALEZ 1986). This is probably related to the type of

The regression between body weight and linear body measurements of two ibex populations and one chamois population

	Regression equation	R^2	n	Syx	95 %	F	DF	P
	Ibex cazorla							
Male	weight = 13.20 + 0.07 HORN	0.81	45	6.00	1.79	175.13	1–43	<0.01
	weight = –43.4 + 0.07 LCC	0.79	43	6.87	2.20	158.10	1–41	<0.01
	weight = –57.1 + 0.12 PTOR	0.77	25	4.14	1.70	81.34	1–23	<0.01
Female	weight = 4.78 + 0.16 HORN	0.70	36	4.73	1.60	79.22	1–34	<0.01
	weight = –33.4 + 0.06 LCC	0.86	34	2.91	0.76	214.31	1–32	<0.01
	weight = –24.1 + 0.07 PTOR	0.81	17	4.47	2.29	65.57	1–15	<0.01
	Ibex gredos							
Male	weight = 11.39 + 0.08 HORN	0.86	45	6.03	1.78	272.72	1–43	<0.01
	weight = –65.8 + 0.10 LCC	0.82	49	7.03	2.03	224.59	1–47	<0.01
	weight = –45.5 + 0.10 PTOR	0.81	49	8.10	2.31	207.49	1–47	<0.01
Female	weight = 8.75 + 0.12 HORN	0.79	39	4.75	1.53	136.36	1–37	<0.01
	weight = –34.1 + 0.09 LCC	0.82	39	3.25	1.23	169.39	1–37	<0.01
	weight = –26.1 + 0.07 PTOR	0.77	39	5.06	1.64	123.12	1–37	<0.01
	Chamois							
Male	weight = 4.22 + 0.11 HORN	0.75	23	2.66	1.15	67.67	1–21	<0.01
	weight = –22.2 + 0.04 LCC	0.84	26	1.35	0.54	142.04	1–24	<0.01
	weight = –19.1 + 0.06 PTOR	0.86	26	2.35	0.94	162.16	1–24	<0.01
Female	weight = 8.02 + 0.09 HORN	0.60	21	1.57	0.71	28.79	1–19	<0.01
	weight = –14.4 + 0.03 LCC	0.65	21	2.34	1.06	36.91	1–19	<0.01
	weight = –19.3 + 0.06 PTOR	0.68	18	1.41	0.70	36.80	1–16	<0.01

R^2 = Coefficient of estimate; n = specimens number; Syx = Standard error of estimate; 95 % = Confidents limits; F = Variance ratio; DF = Degrees of freedon; P = Probability of zero-slope. (HORN = Horn length, LCC = body length, PTOR = Chest girth)

sexual selection which favors the development of secondary sexual characteristics, mainly related to fighting (Schaffer and Reed 1972; Clutton-Brock et al. 1980).

The relationship between horn-length and body weight gives a higher correlation index in males than in females of the two species considered. Nievergelt (1966) found similar results for the Alpine ibex where the length of the horn showed the greatest correlation with body weight of males.

Regressions between horn length and body weight have been reported in other bovids (Gray and Simpson 1979; Bunnell 1980; Popp 1985). In this study, differences in the degree of fitness of horn length/body weight regression were found. These differences can be seen at three levels; specific (Ibex specimens showing higher fitness than the Chamois), sexual (males having higher fitness than females), or population in Ibex females specimens, from Gredos being better fited than those from Cazorla. On the other hand, other studies (Fandos 1986; Fandos and Vigal in press) suggested that the annual growth rate also shows differences connected with species, sex or population. Thus, we conclude from these two facts, that annual growth rate could be related to the degree of fitness of this regression.

A second reason why ibex shows a high correlation between body weight and horn length, can be explained by the methods used in the present study. The sample of specimens studied was considered to be sufficiently representative of the population concerning sex and age aspects, trying to avoid the error described by Bunnell (1980) which occurs when all the age groups are not included in the sample. It must also be pointed out that these specimens were collected throughout the whole year, thus avoiding seasonal variations (Gray and Simpson 1979).

Chest girth measurement (PTOR) provides the best estimate of body weight in the chamois in both sexes. Similar results for this species have been obtained by Schroeder and Redlich (1976). However, R^2 values between these two measurements (0.86 and 0.68; table) is lower than the one obtained by Bunnell (1980) for the mountain goat *(Oreamnus americanus)*.

In chamois, when estimating body weight from the three variables, R^2 value for females was lower than for males (Table). This fact may be related to the higher energetic expenses of reproduction (gestation and suckling) in females, as suggested by Gray and Simpson (1979) to explain the rates of development of horns in the Barbary sheep *(Ammotragus lervia)*.

Acknowledgements

We would like to thank B. Cook and S. Reig for their help in translating the manuscript into an English version.

Zusammenfassung

Gewichtsabschätzungen für den spanischen Steinbock, Capra pyrenaica und die Gemse, Rupicapra rupicapra (Mammalia, Bovidae)

Es wurde das Verhältnis zwischen Körpergewicht und den Maßen für Hornlänge, Brustumfang und Körperlänge für den spanischen Steinbock, *Capra pyrenaica* (Schinz, 1838) und die Gemse, *Rupicapra rupicapra* (L., 1758), analysiert. Für jede Population und für beide Geschlechter waren getrennte Berechnungen linearer Regressionen notwendig. Alle Beziehungen sind statistisch signifikant ($p < 0.01$). Die besten Voraussagen über das Körpergewicht erlauben für den männlichen Steinbock die Hornlänge, für den weiblichen Steinbock die Körperlänge sowie der Brustumfang für beide Geschlechter der Gemse.

References

Blood, D. A.; Lovaas, A. L. (1966): Measuremets and weight relationships in Manitoba elk. J. Wildl. Manage. **30**, 135–140.

Bunnell, F. L. (1978): Horn growth and population quality in Dall sheep. J. Wildl. Manage. **42**, 755–764.

— (1980): Weight estimation of Dall's sheep and mountain goat. Wildl. Soc. Bull. **8,** 291–297.
Clutton-Brock, T. H.; Albon, S. D.; Harvey, P. H. (1980): Antlers, body size and breeding group size in the Cervidae, Nature **258,** 565–567.
Fandos, P. (1986): Aspectos ecológicos de la población de cabra montés en las Sierras de Cazorla y Segura, Jean. Thesis Doc. Universidad Complutense, Madrid, 1–475 p.
Fandos, P.; Vigal, C. R. (in press): Body weight and horn length in relation to age of the Spanish wild goat. Acta theriol.
Fernandez-Lopez, J. M.; Garcia Gonzalez, R. (1986): Craniométrie comparée entre les chamois pyrénéen et cantabrique. Mammalia **50,** 87–97.
Geist, V. (1966): The evolutionary significance of mountain sheep horns. Evolution **20,** 558–566.
Gray, G. C.; Simpson, C. D. (1979): Weight estimation of Babary sheep from horn length. Wildl. Soc. Bull. **7,** 285–288.
Hall-Martin, A. J. (1977): Giraffe weight estimation using dissected leg weight and body measurements. J. Wildl. Manage. **41,** 740–745.
McEwan, E. H.; Wood, A. J. (1966): Growth and development of the barren ground caribou. I. Heart girth, hind foot length, and body weight relationships. Can. J. Zool. **44,** 401–411.
Nievergelt, B. (1966): Der Alpensteinbock (*Capra ibex* L.) in seinem Lebensraum. Mammalia depicta 1. Hamburg, Berlin: Paul Parey.
Popp, J. W. (1985): Horn and body size among antelopes. Säugetierkde. Mitt. **32,** 245–248.
Rideout, C. B.; Worthen, C. L. (1975): Use of girth measurement for estimating weight of mountain goats. J. Wildl. Manage. **39,** 705–708.
Ross, J. G. (1958): A method of estimating live weights in small shorthorn zebu cattle from linear body measurements. E. Afr. Agric. J. **23,** 193–194.
Schaffer, W. M.; Reed, C. A. (1972): The co-evolution of social behavior and cranial morphology in sheep and goats (Bovidae, Caprini). Fieldiana: Zoology **61,** 1–88.
Schroeder, W.; Redlich (1976): Untersuchungen an der bayerischen Gams. I. Körpermaße und Gewichte. Tagungsbericht. 2nd. Conf. Internationales Gamswild. Ljubljana.

Authors' addresses: Paulino Fandos, Museo Nacional de Ciencias Naturales, c/Jose Gutierrez Abascal 2, E-28006 Madrid; Carlos R. Vigal and Jose M. Fernandez-Lopez, Unidad de Zoologia Aplicada, Comunidad Autónoma de Madrid, Aptdo 127, El Encín, Alcala de Henares, Madrid 1, España

Z. Säugetierkunde 54 (1989) 243–250

ISSN 0044-3468

Genetic variation in the Alpine chamois, with special reference to the subspecies *Rupicapra rupicapra cartusiana* Couturier, 1938

By J. M. Pemberton, P. W. King, S. Lovari, and V. Bauchau

Department of Zoology, University College London, London, UK

Receipt of Ms. 1. 2. 1988

Abstract

Genetic variation in 53 individuals representing 6 Alpine chamois *(Rupicapra rupicapra)* populations was investigated by starch gel electrophoresis, in order to determine the extent to which the endangered subspecies *R. r. cartusiana* differs from *R. r. rupicapra* and merits protection. Across all populations studied 10 of 55 loci screened were polymorphic and average heterozygosity was typical for a mammal but high for a large mammal. As measured by Nei genetic distances, the *cartusiana* population was the most distinct, but no loci diplaying fixed differences between populations were detected. It is concluded that the decision to protect the *cartusiana* population must depend on the cost of the protection.

Introduction

Chamois (genus *Rupicapra*) occur in mountainous regions of Central Europe and the Near East. In a recent taxonomic revision, two species were proposed, *R. rupicapra,* containing Alpine, Eastern European and Asian chamois and *R. pyrenaica* containing chamois native to the Cantabrain Mountains, Pyrenees and Apennines (Nascetti et al. 1985). Ten subspecies of chamois have been described (Couturier 1938; Lovari and Scala 1980), and this paper concentrates on the status and survival of one, *R. r. cartusiana.*

The subspecies *R. r. cartusiana* (hereafter referred to as *cartusiana*), named after the Chartreuse region of France, was described by Couturier (1938) who separated it from the geographically close *R. r. rupicapra* (hereafter referred to as *rupicapra*)on the basis of its horn shape, stockier build, darker winter coat colour and a series of skull traits (characteristics of the nasal and lacrymal bones, a long and narrow ethmoidal fissure and long premolar and molar tooth rows). At present, the population of the *cartusiana* subspecies is of unknown purity because of previous introductions (C. Berducou, pers. comm.) and numbers not more than 100 individuals (F. Roucher, pers. comm.). Furthermore, assuming that the *cartusiana* population is genetically distinct, its identity is under threat from two sources. First, a neighbouring, introduced, *rupicapra* population may expand further into the *cartusiana* area (see Fig. 1) and second, some local hunters hope to introduce more *rupicapra* within the current *cartusiana* range. In either case, the two subspecies might hybridize and the identity of the *cartusiana* subspecies might be lost for ever. The *cartusiana* population is rated as 'endangered' by I.U.C.N. (1986).

The aim of this study was to test the assumption, made in the previous paragraph, that the *cartusiana* population is genetically distinct from *rupicapra* populations and, if the populations proved different, to measure how different they are. This information could then be used in planning conservation measures for the *cartusiana* population.

As an objective method of measuring genetic variation, we used protein electrophoresis. In previous electrophoretic studies, several polymorphic loci have been identified in chamois (Nascetti et al. 1985; Miller and Hartl 1986; 1987).

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5404-0243 $ 02.50/0

Material and methods

Samples of muscle (M), liver (L), kidney (K) and heart (H) (with some exceptions, see below) were collected by hunters in the course of normal hunting operations. The tissues were removed soon after the animals were dead and stored at −20 °C until processed for electrophoresis. Samples were collected from the *cartusiana* population itself, from four nearby *rupicapra* populations (see Fig. 1) and from one distant *rupicapra* population (Lombardia, Italy). Only muscle samples were obtained from the Lombardia population. Sample sizes are shown in Table 1.

Tissue samples were homogenized in buffer and centrifuged. The supernatants were loaded onto gels. Horizontal starch gel electrophoresis was carried out by conventional techniques, generally

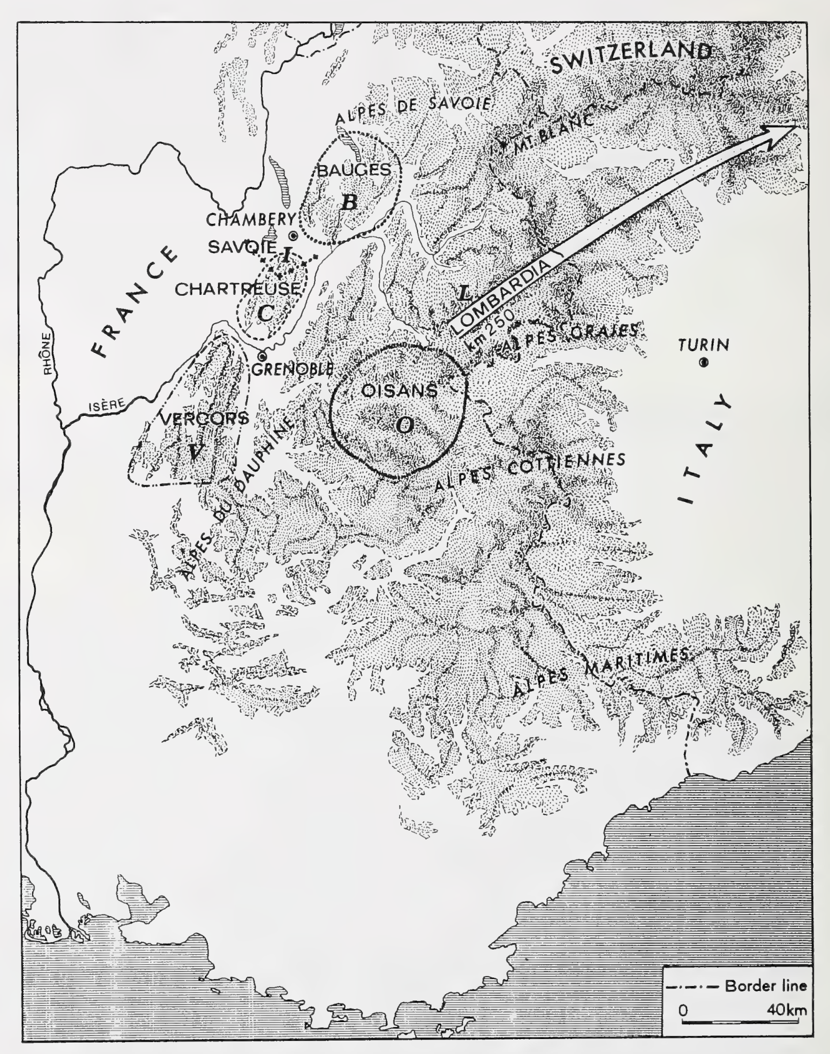


Fig. 1. Map of part of the French Alps, showing location of the *R. r. cartusiana* population (C) and of the neighbouring *R. r. rupicapra* populations which we sampled. Letters indicate sampling sites as coded in Table 1. The letter I indicates the population of introduced *R. r. rupicapra* which lives in the Chartreuse-Savoie region. This population was founded with 25 individuals from the Bauges (B) population and 4 individuals of Austrian ancestry (F. Roucher, pers. comm.). The Lombardia, Italy, sampling site lies approximately 250 km North East of the region shown

following buffer systems and staining recipes given by Harris and Hopkinson (1976). The loci screened are listed below in the results section.

Relationships between the populations screened were studied by calculating genetic distances (Nei 1972) and conducting median hierarchical cluster analysis on the genetic distances using the SAS package (SAS Institute 1985).

Results

Where all four tissue types were available from an individual, we attempted to screen a total of 70 different loci. In the listings below, we have adopted the following conventions. Locus designations (−1, −2, −3) follow the notation of Allendorf and Utter (1979) in which loci are numbered starting from the most cathodal seen. Additional descriptions are given in some cases. Peptidases are designated according to the substrate used (see Harris and Hopkinson 1976). The symbols M, L, K and H after a locus indicate the tissue from which we preferred to score (or in the case of the first paragraph below, attempted to score) a particular locus. Because we had only muscle samples from the Lombardia population, many loci which we normally scored from other tissues were scored from muscle in the Lombardia population (indicated by a 'M' after the first choice tissue). For loci where no 'M' appears at all, we were unable to screen the Lombardia samples.

A total of 15 loci which we attempted to screen proved unsatisfactory because of insufficient enzyme activity or poor resolution of bands on the gel. These loci were acid phosphatase-3 (ACP-3, K), alcohol dehydrogenase (ADH, L), aldolase (ALD, M), diaphorase-1 and -2 (DIA-1, K, M and DIA-2, K, M), enolase (ENO, M), guanine deaminase (GDA, L, M), hexokinase-1, (HK-1, K, M), α-glycerophosphate dehydrogenase-2, (αGPD-2, H, M), inorganic pyrophosphatase (PP, M), peptidase-D and -E (PEP-D, K and PEP-E, K), phosphoglucomutase-3 (PGM-3, K), phosphoglycolate phosphatase (PGP, M) and xylose dehydrogenase, XLD, L).

No variation was found at 45 loci screened. These loci were acid phosphatase-1 and -2 (ACP-1, K and ACP-2, K, M), aconitase-2 (ACON-2, K), adenylate kinase-1 and -3 (AK-1, H, M and AK-3, H, M), creatine kinase-1 and -2 (CK-1, H, M and CK-2, H), liver esterase-1 and -2 (L-EST-1, L and L-EST-2, L), muscle esterase-2 (M-EST-2, M), ultraviolet esterase-1 and -2 (UV-EST-1, L and UV-EST-2, L) fructose diphosphatase-1 and -2 (FDP-1, M and FDP-2, L), fumarate hydratase (FH, L, M), glucose dehydrogenase (GDH, L, M), glucose-6-phosphate dehydrogen-

Table 1. **Allele frequencies at each polymorphic locus in each chamois population sampled, with average heterozygosities based on 55 and 43 loci**

Sample Site	Code	No. of animals	Polymorphic loci [commonest allele (s)]												$\overline{H}$ (55)	$\overline{H}$ (43)
			ACON-1 (S)	(F)	ADA (S)	AK-2 (F)	M-EST-1 (S)	GOT-2 (S)	ME-1 (S)	NP (S)	PEP-B (S)	PGM-2 (M)	(F)	6PGD (F)		
Chartreuse Savoie	I	11	0.60	0.40	0.91	1.00	1.00	0.96	0.91	1.00	0.82	0.50	0.50	0.77	0.042	0.039
Oisans	O	4	0.50	0.50	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.50	0.25	0.75	0.039	0.036
Bauges	B	11	0.95	0.05	0.96	1.00	1.00	0.82	0.90	1.00	0.68	0.59	0.18	0.73	0.037	0.034
Vercors	V	6	0.67	0.33	1.00	1.00	1.00	1.00	0.42	1.00	0.67	0.90	0.10	1.00	0.042	0.043
Lombardia	L	14	0.25	0.64	0.54	1.00	0.93	1.00	1.00	0.93	1.00	–	–	0.89	–	0.053
Chartreuse	C	7	0.93	0.07	0.71	0.93	0.93	1.00	0.71	1.00	0.64	0.64	0.36	0.21	0.049	0.050

ase (G6PD, K, M), glucose phosphate isomerase (GPI, K, M), glutamate oxaloacetate transaminase-1 (GOT-1, K, M), glutamate pyruvate transaminase (GPT, L, M), glutathione reductase (GR, K, M), glyceraldehyde phosphate dehydrogenase (GAPDH, H, M), α-glycerophosphate dehydrogenase-1 (α-GPD-1, H, M), hexokinase-2 and -3 (HK-2, K, M and HK-3, K, M), isocitrate dehydrogenase-1 and -2 (IDH-1, K, M and IDH-2, K, M), NAD-dependent isocitrate dehydrogenase (NAD-IDH, H, M), lactate dehydrogenase-1 and -2 (LDH-2, H, M and LDH-2, H, M), malate dehydrogenase-1 and -2 (MDH-1, K, M and MDH-2, K, M), malic enzyme-2 (ME-2, H, M), mannose phosphate isomerase (MPI, L, M), peptidase-A and -C (PEP-A, M and PEP-C, M), phosphoglucomutase-1 (PGM-1, K, M), phosphoglycerate kinase (PGK, K, M), phosphoglyceromutase-1 and -2 (PGAM-1, K, M and PGAM-2, K, M), pyruvate kinase-1 and -2 (PK-1, M and PK-2, L), sorbitol dehydrogenase (SDH, L, M) and superoxide dismutase-1 and -2 (SOD-1, H, M and SOD-2, H, M).

Polymorphism was found at 10 loci screened. These loci were aconitase-1 (ACON-1, K, M), adenosine deaminase (ADA, H, M), adenylate kinase-2 (AK-2, H, M), muscle esterase-1 (M-EST-1, M), glutamate oxaloacetate transaminase-2 (GOT-2, K, M), malic enzyme-1 (ME-1, H, M), nucleoside phophorylase (NP, L, M), peptidase-B (PEP-B, M), phosphoglucomutase-2 (PGM-2, L) and 6-phosphogluconate dehydrogenase (6PGD, K, M).

At most polymorphic loci we found two alleles. We called the most anodal F for fast and the less anodal S for slow. At PGM-2 and ACON-1 we found three alleles, so there was also a M for medium allele. All band patterns observed were consistent with the known quaternary structure of the enzymes involved. Observed allele frequencies and mean heterozygosity levels for each population are shown in Table 1.

From the electrophoretic data obtained we calculated Nei's genetic distances between each pair of populations screened, and we used median hierarchical cluster analysis to construct dendrograms showing the genetic relationships between populations. We performed these calculations twice, firstly including all 10 polymorphic and 45 monomorphic loci screened but on the French populations only, and secondly, in order to include the Italian population, we based the calculations on those loci which we were able to screen in muscle samples only. This reduced the sample of loci to 9 polymorphic loci plus 34 monomorphic loci. Genetic distances are shown in Table 2 while dendrograms illustrating genetic relationships between populations are shown in Fig. 2. In both analyses, the *cartusiana* population is genetically the most distinct of the populations screened.

Discussion

Among the French chamois studied, the population of the putative *cartusiana* subspecies (C) is genetically the most distinct (Table 2 and Fig. 2a). The Italian population screened (L) is of particular interest because, given its distant location from the French populations studied, one might expect it to be genetically distant from all of them as a result of local drift and selection processes. Contrary to this idea, when the Italian population is included in the analysis, it groups with the majority of the French populations, leaving the *cartusiana* population once again the most distinct (Table 2 and Fig. 2b).

How different is the *cartusiana* population from the *rupicapra* populations studied? If our electrophoretic study had shown that the *cartusiana* population grouped within the other French populations in the genetic distance dendrograms (Fig. 2), we would have demonstrated that there was essentially no difference between the *cartusiana* and *rupicapra* populations. If, on the other hand, we had found loci at which there were fixed differences between *cartusiana* and the other populations, we would have demonstrated a large difference between *cartusiana* and the *rupicapra* populations. In fact, we have found a

Table 2. **Genetic distances (Nei) between the chamois population studied**

Figures above the diagonal are based on 55 loci, while figures below the diagonal are based on the 43 loci which could be screened from muscle samples alone

Population	I	O	B	V	L	C
I		0.002	0.005	0.009	---	0.011
O	0.001		0.007	0.012	---	0.016
B	0.004	0.008		0.009	---	0.008
V	0.008	0.013	0.010		---	0.018
L	0.007	0.007	0.019	0.020		---
C	0.013	0.019	0.010	0.021	0.027	

situation between these two extremes. The *cartusiana* population is the most distinct studied, but the differences detected are all in allele frequencies. In a large sample of loci (55), we found none with fixed differences between *cartusiana* and *rupicapra*, and only one at which the *cartusiana* population has a different allele segregating (AK-2, and this was only in a single animal).

A second way to look at the data is to consider whether it supports the idea that the *cartusiana* population is a separate chamois subspecies. The subspecies classification is generally subjective and unsatisfactory and there are no objective rules for identifying a subspecies on the basis of genetic distances found from electrophoretic data. However, it is interesting to look at data from other species. Perhaps the most relevant study is the electrophoretic study of European red deer conducted by GYLLENSTEN et al. (1983). In this study, genetic distances were compared between red deer of different named subspecies (which were originally separated on the basis of morphology). The survey involved 594

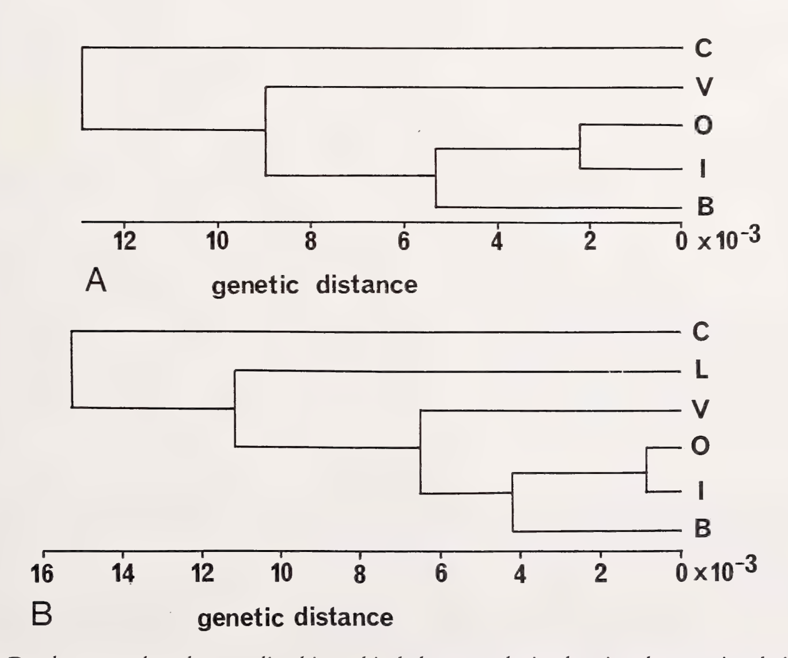


Fig. 2. Dendrograms, based on median hierarchical cluster analysis, showing the genetic relationships between the chamois populations studied. Site codes are as shown in Table 1. A: Shows the 5 French populations screened and is based on 55 loci, while B also includes the Italian Lombardia population studied and is based on the 43 loci which could be screened out of muscle samples

samples from 22 localities and 34 loci. Genetic distances between subspecies were variable but low compared with other investigated examples and the mean was 0.0164. The mean genetic distance between *rupicapra* and *cartusiana* populations in our study is 0.0133 (based on 55 loci but excluding Lombardia) or 0.0180 (based on 43 loci and including Lombardia). So the genetic distance between *rupicapra* and *cartusiana* is of the same order of magnitude as the distance between named red deer subspecies.

A third way to look at the data is to consider the amount of variation present in each population studied, by examining the average heterozygosity estimates given in Table 1. One might expect that the *cartusiana* population, being small and historically relatively isolated, would have lower levels of variation than other populations. However, among estimates based on either 55 or 43 loci, the *cartusiana* population has the highest estimated average heterozygosity among all the French populations studied. Only the Italian population, when included, has a higher estimated average heterozygosity.

To summarise the situation, we believe that the *cartusiana* population is genetically different from the *rupicapra* populations, and that for those who regard the subspecies status as important, the differences are large enough to justify calling the *cartusiana* population a separate subspecies. If the *cartusiana* population is protected, some of the existing genetic diversity of chamois will be maintained. Genetic diversity is probably important for the evolutionary survival of a species (Frankel and Soulé 1981). This benefit must be compared with the cost of protection. Protection would consist of, for example, stopping hunting of the *cartusiana* population for some time, preventing natural spread of *rupicapra* into the *cartusiana* population and not deliberately introducing a *rupicapra* population into the *cartusiana* range. We do not know what the costs of such protection would be, and so the cost-benefit comparison and the final decision is up to the French authorities. However, of the three protection measures mentioned, we feel that it would be very difficult to justify the deliberate introduction of a *rupicapra* population into the *cartusiana* range.

Our conclusions may be criticized because our sample sizes for each population are small. However, in general, estimates of genetic distances and average heterozygosities are more sensitive to the number of loci studied than to the number of individuals studied (Nei 1978; Gorman and Renzi 1979) and we have studied a relatively large number of loci (55). We would like to have had samples from more individuals, especially of the *cartusiana* population. However, we would not like to encourage further hunting of an endangered population simply to obtain further samples. Small sample sizes are likely to be a common problem when laboratory techniques are applied to conservation problems, and the limitations of sample size should be considered before such studies begin.

There have been three previous studies of electrophoretic variation in chamois. Nascetti et al. (1985) found 7 of 25 loci screened were polymorphic in samples from 5 populations (including 2 from the proposed *R. pyrenaica* species), and average heterozygosities ranging from 0.000–0.033. Miller and Hartl (1986) found 8 of 41 loci were polymorphic in two Austrian populations, and average heterozygosities of 0.046 and 0.056. In a further survey of Austrian populations, Miller and Hartl (1987) found 10 out of 42 loci were polymorphic, with average heterozygosities ranging from 0.035–0.047 (this data is also summarized in Hartl [1986]). In our study we found 10 out of 55 loci were polymorphic and average heterozygosities ranging from 0.034 to 0.053. Although the overall figures from the Austrian studies and our own are pleasingly similar, the Italian study differs strikingly and there are in fact many differences of detail among the various studies. We do not propose to discuss these in detail, but we suggest that three factors are responsible. First, the different groups have studied different populations of chamois, which may be expected to differ genetically. Second, the different groups have studied different combinations and numbers of loci, which are bound to influence estimates of the level of variation (Gorman and Renzi 1979; Hartl 1985). Third, the different groups

may well have different levels of skill or standards. For example, although Miller and Hartl (1986, 1987) found polymorphism at ACP-3 and PGM-3, we were unable to resolve these systems satisfactorily enough to score them. Nevertheless, we hope at some stage to be able to combine all the existing data sets to carry out a larger analysis of chamois populations.

Our results and those of Miller and Hartl (1986, 1987) suggest that alpine chamois retain high levels of genetic variation compared with other large mammals. In a survey of electrophoresis studies of 184 species of mammal, Nevo et al. (1984) found that the mean average heterozygosity was 0.041 +/− 0.035 (S. D.). The average heterozygosity estimates given for Austrian and French chamois in the paragraph above suggest that alpine chamois have levels of variation close to the mean for all mammals. For reasons which are poorly understood, large mammals tend to have lower average heterozygosities than small mammals (Wooten and Smith 1984; Nevo et al. 1984), so chamois are unusual among large mammals in having such high average heterozygosities.

Note added in proof

Under the auspices of the Office National de la Chasse, France, a similar selection of samples to ours has been screened electrophoretically by F. Bonhomme, Institut des Sciences de l'Evolution, Montpellier, France, and the results have recently become available. The survey was based on 25 loci and no evidence was found that the *cartusiana* population differed from neighbouring populations (C. Berducou and F. Bonhomme, pers. comm.). We believe this difference from our study emphasizes the points we make in our discussion regarding the identity of loci studied, the differences in techniqes used in different laboratories and, especially, the need to study a large number of loci.

Acknowledgements

We thank M.-H. Cruveille, M. Michaller, F. Roucher and G. Tosi for providing the samples and backing our study, Professor R. J. Berry, in whose laboratory the electrophoresis was carried out and D. Jenkins for translating the summary.

Zusammenfassung

Die genetische Variabilität der Alpengemse mit besonderer Berücksichtigung der Unterart Rupicapra rupicapra cartusiana Couturier, 1938

Die genetische Variabilität von 53 Gemsen *(Rupicapra rupicapra)* aus sechs Populationen in den Alpen wurde mit Hilfe der Stärkegel-elektrophorese geschätzt. Geklärt werden sollte vor allem, wie weit sich die gefährdete Unterart *R. r. cartusiana* von *R. r. rupicapra* unterscheidet und Schutz verdient. 10 der insgesamt 55 untersuchten Genloci waren polymorph. Die durchschnittliche Heterozygotierate war für Säugetiere insgesamt typisch, für Großsäuger aber hoch. In den nach Nei berechneten genetischen Distanzen bilden die Tiere von *cartusiana* die am stärksten isolierte Population, wenn auch für keinen Genlocus ein völlig fixierter Unterschied gefunden wurde. Daraus wird gefolgert, daß der Schutz von *cartusiana* von den dadurch entstehenden Kosten abhängig gemacht werden sollte.

References

Allendorf, F. W.; Utter, F. M. (1979): Population genetics. In: Fish Physiology. Ed. by W. S. Hoar, D. J. Randall and J. R. Brett. New York: Academic Press. Vol. **8**, 407–454.

Couturier, M. (1938): Le Chamois. Grenoble: Arthaud.

Frankel, O. H.; Soulé, M. E. (1981): Conservation and Evolution. Cambridge: Cambridge Univ. Press.

Gorman, G. C.; Renzi, J. (1979): Genetic distance and heterozygosity estimates in electrophoretic studies: effects of sample size. Copeia 1979, 242–249.

Gyllensten, U.; Ryman, N.; Reuterwall, C.; Dratch, P. (1983): Genetic differentiation in four European subspecies of red deer (*Cervus elaphus* L.). Heredity **51**, 561–580.

Harris, H.; Hopkinson, D. A. (1976): Handbook of enzyme electrophoresis in human genetics. Amsterdam: North-Holland Publishing Co.

Hartl, G. (1985): Auffällige Unterschiede in der genetischen Variabilität freilebender Großsäuger und ihre möglichen Ursachen. Z. Jagdwiss. **31,** 193–203.

— (1986): Steinbock und Gemse im Alpenraum – genetische Variabilität und biochemische Differenzierung zwischen den Arten. Z. zool. Syst. Evolut.-forsch. **24,** 315–320.

I.U.C.N. (1986): 1986 I.U.C.N. Red list of threatened animals. Gland, Cambridge: I.U.C.N.

Lovari, S.; Scala, C. (1980): Revision of *Rupicapra* genus, 1. A statistical re-evaluation of Couturier's data on the morphometry of six chamois subspecies. Boll. Zool. **47,** 113–124.

Miller, C.; Hartl, G. B. (1986): Genetic variation in two alpine populations of chamois, *Rupicapra rupicapra* L. Z. Säugetierkunde **51,** 114–121.

— — (1987): Genetische Variabilität bei Gemsen der Alpen (*Rupicapra rupicapra* L.). Z. Jagdwiss. **33,** 220–227.

Nascetti, G.; Lovari, S.; Lanfranchi, P.; Berducou, C.; Mattiuci, S.; Rossi, L.; Bullini, L. (1985): Revision of *Rupricapra* genus. III. Electrophoretic studies demonstrating species distinction of chamois populations of the Alps from those of the Apennines and Pyrenees. In: The Biology and Management of Mountain Ungulates. Ed. by S. Lovari. London: Croom Helm. 56–62.

Nei, M. (1972): Genetic distance between populations. Am. Nat. **106,** 283–292.

— (1978): Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics **89,** 583–590.

Nevo, E.; Beiles, A.; Ben-Shlomo, R. (1984): The evolutionary significance of genetic diversity: ecological, demographic and life history correlates. In: Evolutionary Dynamics of Genetic Diversity. Ed. by G. S. Mani. Berlin: Springer-Verlag. Lecture Notes in Biomathematics **53,** 13–213.

SAS Institute (1985): SAS User's Guide: Statistics. Cary: N. C. SAS Institute Inc.

Wooten, M. C.; Smith, M. H. (1984): Large mammals are genetically less variable? Evolution **39,** 210–212.

Authors' addresses: Dr. J. M. Pemberton, Department of Genetics, Downing Street, Cambridge, CB2 3EH, U.K.; P. W. King, Department of Zoology, University College London, Gower Street, London WC1E 6BT, U.K.; Prof. S. Lovari, Zoologia e Anatomia comparata, Dipartimento di Biologia Cellulare, Universita' Degli Studi di Camerino, via F. Camerini, 2, I-62032 Camerino, Italy, and Dr. V. Bauchau, Labo FYAD, Universite Catholique de Louvain, Place Croix du Sud 2, B-1348 Louvain-la-Neuve, Belgium

Z. Säugetierkunde 54 (1989) 251–260

ISSN 0044-3468

The effect of overgrazing on the small mammals in Umfolozi Game Reserve

By A. E. Bowland and M. R. Perrin

Department of Zoology, University of Natal, Pietermaritzburg, South Africa

Receipt of Ms. 25. 11. 1987

Abstract

Four trapping grids in two open woodland communities were monitored from July 1982 to December 1983. Small mammal population numbers showed a positive response to a decrease in large ungulate grazing pressure. Diversity indexes of the small mammal community varied with woodland type and ungulate grazing pressure. Certain factors suggested that the quantity of cover is of prime importance to the density and diversity of small mammals but when cover reached threshold levels the degree of plant species diversity became important. Disparate vegetation recovery after rain indicated that small mammals respond to cover improvement rather than rain itself.

Recruitment and breeding condition seemed to be inhibited by the effects of overgrazing. Each sex of *Praomys natalensis, Saccostomus campestris,* and *Aethomys chrysophilus* was similarly affected by the impact of overgrazing. Long term recapture rates were higher in zones with less grazing and more cover. The average distance between captures of *P. natalensis* in the overgrazed areas was relatively greater than in regions with reduced grazing pressure while that of *S. campestris* seemed unaffected by cover condition. Mobility of *P. natalensis* was probably influenced by an interaction of small mammal density and cover condition. The 1982/3 drought caused population densities of small mammals throughout the study area to „crash".

Introduction

Grazing by large herbivores influences many aspects of grassland ecosystems including vertical structure, plant species composition and diversity, and standing crop of plant biomass. The impact on the grass and forb layer, or herb layer, by wild grazing ungulates in their natural habitats has been investigated by numerous workers.

McNaughton (1976) showed that over a four-day period the grazing of migrant wildebeest reduced green biomass by 84.9 % and grass height by 56.0 %. Emslie (1982) reported that at Umfolozi Game Reserve (UGR) the standing biomass of the herb layer in a heavily grazed area of *Acacia nigrescens* open woodland was 20.0 % that of a paired site with about half the grazing ungulate stocking level.

Emslie 1983 (pers. comm.) recorded 33 % of the offtake of *Panicum coloratum* (Graminae) and 23 % of the offtake of *Themeda triandra* (Graminae) could be accounted for by insects in the non-cull block in 1981–82. He further estimated that between 35 and 40 % of the total grazing occurring in UGR in 1981–82 was by invertebrates. During the drought in 1982–83 harvester termites were the major grazers over large areas in the non-cull block.

Delany (1964) noted that the species and biomass of small rodents varied with the extent of large mammal grazing. In the savanna of the Crater area (Uganda), with little grazing by large mammals, nine species of small mammals were recorded. A few miles distant at Mweya Peninsula where grazing by buffalo and elephant was extensive only four rodent species were recorded. The rodent biomass in the latter region was only about one quarter of the former.

French et al. (1976) and Grant and Birney (1979) have related the importance of the density of above-ground plant biomass to small mammals abundance and distribution.

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5404-0251 $ 02.50/0

GRANT et al. (1982) showed that grazing had a direct effect on the structure and productivity of small mammal communities.

Grazers, both vertebrate and invertebrate, can modify the herb layer in terms of structure and species composition to a level where small mammals are affected. Overutilisation of the herb layer by grazers may influence small mammal dynamics in many ways, shelter and food supply are reduced by cover removal while exposure to predation is enhanced.

The aim of this project was to determine the impact of overgrazing on small mammals in UGR.

Study area

UGR (28° 12′ to 28° 26′ S, 31° 42′ to 31° 59′ E) covers an area of 47753 ha; two large valleys, sculptured by the Black and White Umfolozi rivers, dominate the undulating topography. Altitudes range from 45–579 m a.s.l. The mean annual rainfall (averaged over 24y) is 680 mm with the wettest months occurring between October and March, although heavy rains sometimes fall in winter. Mist, frost and hail are rare while heavy dew is experienced mainly in autumn and winter (BOURQUIN et al. 1971).

The vegetation in UGR comprises mainly *Acacia* woodland dominated by *Acacia nigrescens, A. tortilis, A. nilotica,* and *A. karroo* open woodlands. Riparian forest, characterised by *Ficus sycomorus* and *A. robusta*, is confined to drainage lines. Closed woodland is usually found on flat, low-lying areas and is characterised by *Spirostachys africana*. The area falls within the Zululand Thornveld subcategory of the Coastal Tropical



Fig. 1. A map of the bi-zonal study area in Umfolozi Game Reserve showing the locations of the trapping grids (1 = *A. nigrescens* non-cull zone, 2 = *A. nigrescens* cull zone, 3 = *A. tortilis* non-cull zone, 4 = *A. tortilis* cull zone

Forest types, and the Lowveld subcategory of the Tropical Bush and Savanna types of ACOCKS (1975).

The study area in the northwestern corner of UGR (Fig. 1) was established for research studies, in particular to test vegetation monitoring techniques. The cull and non-cull zones of the study area provided differing environmental conditions through different ungulate stocking levels. In the cull zone stocking levels of grazing ungulates were reduced to about 50.0 % of the carrying capacity (i.e. to an estimated 9.4 AU/100 ha, where one animal unit (1 AU) = ungulate biomass consuming the same amount of energy as a steer weighing 450 kg, e.g. 6.1 impala = 1.8 zebra = 1 AU) while in the non-cull zone there was no ungulate removal. Advantage was taken of the differing environmental conditions, provided by the cull and non-cull arrangement, to assess the impact of overgrazing on small mammal community ecology.

Materials and methods

Trapping was conducted on 10 × 10 grids with PVC live traps (WILLAN 1978) set at 15 m intervals. A trap was usually placed in the most likely site within one metre of the trap station; the 100 traps in each grid were checked daily in the early morning, rebaited and reset. Each trapping session lasted four consecutive nights thereby giving 400 trapnights per session. Bait comprised a mixture of equal parts rolled oats and peanut butter.

Species, weight, sex, and location on the grid, to facilitate calculation of average distance between captures, were recorded for animals captured. The following criteria were used to evaluate reproductive condition: for females, the state of the vaginal opening (perforate or imperforate) and the condition of the nipples (small, enlarged, lactating); and for males, the position of the testes (scrotal or abdominal). Each animal was individually marked using a toe-clip code before being released at its capture site.

Animals were assigned to age-classes (adult, sub-adult, or juvenile) using body mass as shown in Table 1. The lower limit of the adult class was calculated by subtracting one standard deviation from the mean weight of scrotal or perforate adults, to accommodate animals in an emaciated condition caused by the drought. The average distance between captures of individuals was used to assess the mobility of each species.

Table 1. **Weight categories used to determine age classes of four rodent species**

Species	Females			Males		
	adult (g)	sub-adult (g)	juvenile (g)	adult (g)	sub-adult (g)	juvenile (g)
Praomys natalensis	>33	21–33	<21	>31	21–31	<21
Saccostomus campestris	>36	21–36	<21	>41	21–41	<21
Aethomys chrysophilus	>63	31–63	<31	>71	31–71	<31
Lemniscomys griselda	>47	21–47	<21	>64	21–64	<21

Small mammal populations were estimated using a weighted mean mark-recapture formula (BEGON 1979):

$$\hat{N} = \frac{M_i \times n_i}{(\Sigma m_i + 1)}$$

where $\hat{N}$ = estimate of the population; M_i = number of marked individuals at risk on day i; m_i = number of marked individuals caught on day i; n_i = number of individuals caught on day i.

An index of species diversity was calculated using the following formula (SHANNON 1948):

$$H = \frac{n \log n - f_i \log f_i}{n}$$

where H = species diversity; f_i = number of individuals of one species caught during the trapping session; n = total number of individuals of all species caught during the trapping session.

After exploratory trapping in the study area, two pairs (cull zone vs non-cull zone) of permanent grids were sited in two major vegetation communities viz. *A. nigrescens* and *A. tortilis* open woodlands (Fig. 1).

Data relating to cover was obtained from two sources. First, the species composition and standing biomass of the herb layer was measured by EMSLIE (1982) in April 1982. These data were used to calculate the diversity indexes (Shannon 1948) of the herb layer in each trapping grid. Second, a disc pasture meter (BRANSBY and TAINTON 1977) was used to measure the difference in mean height of the forb layer under *A. tortilis* in the two zones in December 1983.

Results

Trapping results (July 1982–December 1983) are given in Table 2, where population estimates indicate a positive response of small mammal densities to reduced grazing ungulate stocking levels in the *A. nigrescens* open woodland until the population crash caused by the drought. The trend in the *A. tortilis* community is unclear; the small mammal community in both the cull and the non-cull zone responded similarly to the prevalent environmental conditions (ungulate stocking levels and low rainfall).

The diversity indexes and standing biomasses of the herb layer in the four study plots are presented in Table 3. These data show that the herb layer diversity was significantly greater in the nun-cull than in the cull areas in both *Acacia* communities and that the herb layer under *A. tortilis* was more diverse than that under *A. nigrescens* though significantly so only in the non-cull zone.

The diversity indexes of the small mammal communities in the *A. nigrescens* woodland were higher, though not always significantly so, in the cull zone than the non-cull zone.

Table 2. **Small mammal captures, populations estimates (PE), and diversity indexes (DI) in each study grid in Umfolozi Game Reserve from July 1982 to December 1983**

Grid Location	Month	Total captures	PE Animals/ha	DI
A. nigrescens:				
Non-cull	Jul	0	0	–
	Oct	4	0.7	.3
	Nov	3	0.8	.3
	Feb	6	1.7	.4
	Apr	5	2.0	.2
	Oct	1	0	–
Cull	Jul	33	10.7	.4
	Oct	16	6.1	.4
	Nov	11	3.7	.4
	Feb	4	1.5	.3
	Apr	3	0.9	.3
	Oct	0	0	–
A. tortilis:				
Non-cull	Jul	9	3.1	.4
	Oct	32	10.7	.4
	Nov	14	4.6	.4
	Feb	9	3.3	.3
	Apr	19	7.7	.3
	Oct	1	0.3	–
	Dec	2	0.4	–
Cull	Jul	22	8.5	.2
	Oct	28	9.8	.1
	Nov	9	3.2	.2
	Feb	6	2.1	.3
	Apr	15	5.4	.3
	Oct	0	0	–
	Dec	7	6.3	.4

Table 3. **Standing biomasses (from Emslie 1982) and diversity indexes (which are compared, Hutcheson 1970) of the herb layer in the cull and non-cull zones of *A. nigrescens* and *A. tortilis* open woodlands**

		Non-cull		Cull
A. nigrescens	standing biomass g/m² (per EMSLIE 1982)	220		1005
	diversity index (H)	0.95		0.52
	t		15.7	
	v		651	
	p		< 0.001*	
A. tortilis	standing biomass g/m² (per EMSLIE 1982)	330		445
	diversity index (H)	1.0		0.78
	t		6.93	
	v		758	
	p		< 0.001*	
A. nigrescens vs		−8.34		1.78
A. tortilis	t	945		521
	v	< 0.001*		> 0.05
	p			

* Difference significant (at $p < 0.05$).

Table 4. **Species caught, total captures, and a comparison (HUTCHESON 1970) of small mammal diversity indexes in the cull (c) and non-cull (nc) zones in two woodland types during July, October and November 1982**

	A. nigrescens						*A. tortilis*					
	Jul		Oct		Nov		Jul		Oct		Nov	
	nc	c	nc	c	nc	c	nc	c	nc	c	nc	c
P. natalensis	–	22	2	11	2	8	4	20	24	26	6	8
S. campestris	–	1	2	3	–	1	4	1	3	2	7	1
A. chrysophilus	–	2	–	1	–	1	1	–	4	–	–	–
M. minutoides	–	1	–	–	1	–	–	1	1	–	1	–
C. hirta	–	7	–	1	–	1	–	–	–	–	–	–
Total captures	0	33	4	16	3	11	9	22	32	28	14	9
DI =	–	0.43	0.3	0.4	0.28	0.38	0.42	0.16	0.35	0.11	0.39	0.15
t =	–		−1.07		−0.68		2.56		2.69		2.18	
v =	–		16		13		30		58		15	
p	–		>0.2		>0.5		<0.02*		<0.02*		<0.05*	

*Difference significant.

Conversely, the small mammal diversity in the *A. tortilis* cull zone was significantly lower than the non-cull zone (Table 4). Small mammal diversity in the *A. nigrescens* cull zone was significantly higher than the *A. tortilis* cull zone (Table 5).

A comparison of age-structures in the cull and non-cull rodent populations in winter (May and July) and early summer (October and November) showed reduced recruitment in the non-cull zones (Table 6). A clear trend, notwithstanding the small sample sizes, indicates a higher ratio of breeding to non-breeding *P. natalensis* adults in the cull zone. The sex ratios of *P. natalensis, S. campestris,* and *A. chrysophilus* were unaffected by overgrazing; analysis showed no significant differences between the cull and non-cull zones (*P. natalensis* $p > 0.1$; *A. chrysophilus* $p > 0.98$; *S. campestris* $p > 0.98$).

Table 5. **A comparison of small mammal diversity indexes (Hutcheson 1970) in the cull zone of *A. nigrescens (A. nig.)* and *A. tortilis (A. tor.)* open woodlands during July, October, and November 1982**

	July		October		November	
	A. nig.	*A. tor.*	*A. nig.*	*A. tor.*	*A. nig.*	*A. tor.*
Diversity index (from Table 4)	0.43	0.16	0.40	0.11	0.38	0.15
t	2.534		2.685		1.495	
v	50		27		20	
p	< 0.02*		< 0.02*		> 0.1	

* Difference significant.

Table 6. **A comparison (G-test, Sokal and Rohlf 1981) of the winter and summer age structures of *P. natalensis* in the cull and non-cull zones (ratio = ratio of adults to sub-adults and juveniles)**

		Non-cull			Cull	
		n	ratio		n	ratio
Winter:	adult	3	1.0		9	1.0
	sub-adult	3	1.0		38	4.2
	juvenile	2	0.7		18	2.0
	total	8			65	
	G =			19.51		
	p			< 0.001		
Summer:	adult	19	1.0		21	1.0
	sub-adult	12	0.6		23	1.1
	juvenile	0	0		6	0.3
	total	31		*	50	

* Zero frequencies precluded statistical tests.

Table 7. **A comparison (t-test) of the mean distance between captures of *P. natalensis* and *S. campestris* in the cull and non-cull zones over the period July 1982 to April 1983**

Species	Cull			Non-cull					
	n	mean distance (m)	SE	n	mean distance (m)	SE	t	df	p
P. natalensis	52	26.42	2.1	36	36.12	3.7	−2.45	86	< 0.02
S. campestris	7	45.1	9.7	6	34.5	12.6	0.67	11	> 0.5

Table 8. **Recapture rates of all rodent species marked in July and October 1982**

			Jul	Oct	Nov	Feb	Apr	Oct
July:	Cull	n	44	16	5	2	2	0
		%		36.4	11.4	4.6	4.6	
	Non-cull	n	9	6	2	0	0	0
		%		66.7	22.2			
October:	Cull	n		41	8	3	3	0
		%			19.5	7.3	7.3	
	Non-cull	n		33	6	2	1	0
		%			18.2	6.1	3.0	

The average distance between captures of *P. natalensis* was significantly greater in the non-cull zone than in the cull zone while that of *S. campestris* showed no significant difference between zones (Table 7). Long term recapture rates, an indication of survival, were higher in the cull zones (Table 8).

Pasture disc height measurements in the two zones of *A. tortilis* woodland in December 1983, after good spring rains, showed more herb layer in the cull zone (Table 9).

Table 9. **Comparison (t-test) of herb layer heights in the cull and non-cull zones of *A. tortilis* open woodland in December 1983**

Height class cm	Cull		Non-cull
21–25	2		
16–20	5		
11–15	5		
6–10	44		2
1– 5	79		76
0	0		2
n =	135		80
x (cm)	6.15		2.79
SE	0.33		0.14
t =		7.54	
Df =		213	
p		< 0.001	

Discussion

BROOKS (1981) calculated that in the study area grazing ungulate stocking levels in April 1982 were 9.4 AU/100 ha in the cull zone and 17.5 AU/100 ha in the non-cull zone. EMSLIE (1982) in his estimations of herb layer standing biomass in *A. nigrescens* and *A. tortilis* open woodlands in the same area (Table 3) showed clearly more vegetation in the cull zone as a result of the reduced stocking levels.

The ramifications of lower stocking levels and subsequent cover improvement on the small mammal community were reflected in the trapping results. In the *A. nigrescens* open woodland the population estimates and diversity indexes are much higher in the cull zone, with significantly more cover, than in the non-cull zone (Fig. 2, Table 2). The relatively

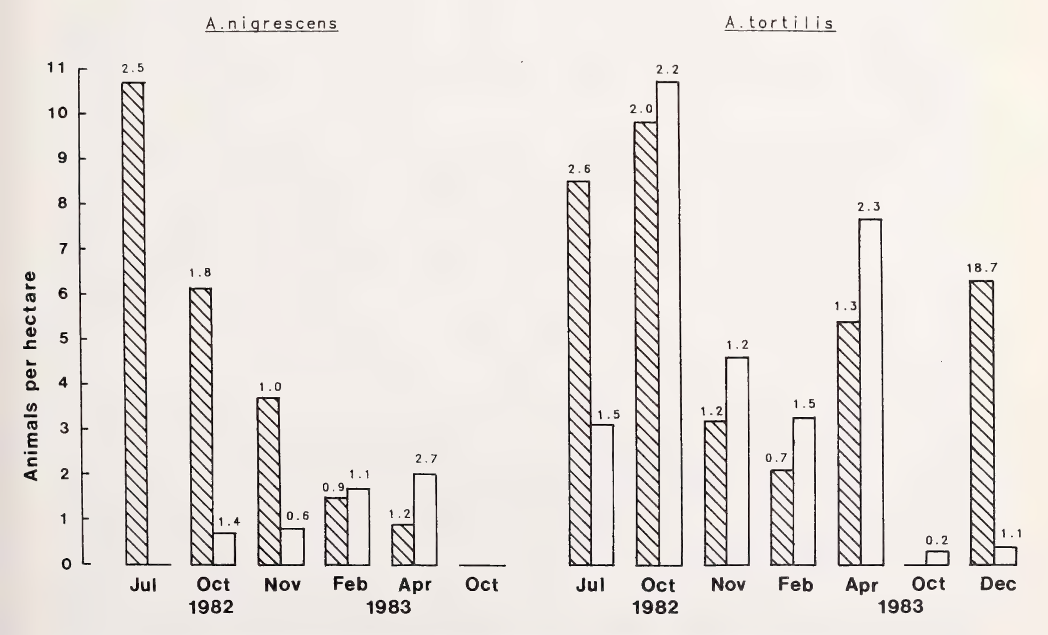


Fig. 2. Population density estimates on the cull and non-cull grids in *A. nigrescens* and *A. tortilis* open woodlands, standard error given above each histogram (▨ = cull zone, ☐ = non-cull zone)

smaller inter-zonal disparity in standing biomass of the herb layer in *A. tortilis* open woodland probably accounts for the generally similar small mammal population densities.

GRANT et al. (1982) found that a reduction in cover in tall-grass grasslands resulted in a decrease in total rodent biomass and suggested some site-specific threshold at which cover is no longer sufficient to support a dense small mammal population. Reduction in vegetative cover in the overgrazed non-cull zone may have brought cover level to or below this threshold level. Small mammal population density estimates on the *A. nigrescens* non-cull grid indicated that cover (standing plant biomass = 220 g/m^2; EMSLIE 1982; Table 3) was probably below the threshold level whereas in both *A. tortilis* zones (standing biomass = 330 g/m^2 – non-cull and 445 g/m^2 – cull; EMSLIE 1982; Table 3) cover may have been at or just above threshold levels. Cover in the *A. nigrescens* cull zone most probably exceeded the threshold level by a comfortable margin which facilitated high small mammal densities before the onset of the drought.

MC'CLOSKEY (1976) reported that in coastal sage scrub in southern California vegetation structure was important in determining small mammal community composition while GRANT et al. (1982) found that in four types of north American grasslands the structural characteristics of the grass community were more important than the plant species composition of the small mammal community. DELANY (1972) provides evidence that small mammal populations and biomass can vary considerably from one grassland type to another, even within different types of woodland savanna; and that greater vegetational heterogeneity is related to a more diverse fauna.

The diversity of the herb layer, measured in terms of species contribution to standing biomass, was significantly greater in the non-cull zones of both woodland communities. The small mammal diversity in the *A. nigrescens* open woodland was greater in the cull zone with its substantial, though less diverse, grass cover. The *A. tortilis* open woodland, with relatively less cover, accommodated a more diverse small mammal community in the vegetatively more diverse non-cull zone. However, the cull zone of the *A. nigrescens* open woodland supported a more diverse small mammal community than that of *A. tortilis* open woodland notwithstanding a more diverse grass community in the latter. These factors suggest that cover quantity is of prime importance to the density and diversity of small mammals but with cover at threshold levels the degree of plant species diversity becomes important.

The response of the herb layer to above average rainfall in October and November 1983 differed in the two zones, in December the mean grass height in the *A. tortilis* non-cull zone was 28 mm while in the cull zone it was significantly higher at 62 mm. Ungulate grazing pressure most probably accounted for the disparate vegetation recovery. By October 1983 all rodent communities were virtually obliterated by drought yet in December some recovery was evident in the *A. tortilis* cull zone (6.3 vs 0.4 animals/ha). That small mammal resurgence was evident only in the zone of substantial cover regeneration suggests that they responded to improved cover conditions rather than the rainfall itself.

Recruitment was inhibited by overgrazing and resultant cover degradation. In winter and summer the proportion of sub-adults and juveniles present in the population is greater in the cull zone than in the non-cull zone. Poor recruitment rate may stem from, firstly, a reduction in fecundity of the adults and, secondly, the juveniles being vulnerable to the harsher conditions (less food, greater exposure to predators and/or climatic extremes) in the non-cull zone. The ratio of breeding to non-breeding adults at the height of breeding season (Oct.–Feb.) is higher in the cull zone. Either the adverse conditions trigger a reproductive inhibitor in the animals or the degraded vegetation precludes an environmental reproductive stimulant. DELANY (1972) suggested that the onset and termination of breeding could be correlated with biochemical and quantitative changes in the diet while SANDERS et al. (1981) found that the reproductive condition in *Microtus montanus* was

initiated by the intake of green shoots containing a cyclic carbomate (6MBOA). In this study heavy grazing pressure by large ungulates would have denied new shoot availability to small mammals thereby inhibiting reproduction.

The greater average distance between captures of *P. natalensis* in the non-cull zone with reduced cover, depleted food resources and lower small mammal densities indicated that mobility may be influenced by an interaction of these factors. The animal has to forage further afield to satisfy basic needs and is allowed to do so because small mammal populations are sparse. The average distance between captures of *S. campestris* was similar in both zones. This animal has a wide habitat tolerance, from sandy open veld, dense bush to forests (De Graaff 1981), and so it is likely that its mobility would be more influenced by food availability and predation than cover condition alone.

The importance of cover to the small mammal community is again emphasised by the greater survival rates, as indicated by long term recapture rates, in the cull zones. Environmental stress on the animals is intensified by cover degradation in terms of food and shelter reduction and increased predation and probably results in decreased longevity.

Acknowledgements

We thank Dr P. M. Brooks for assisting with supervision of this project and Prof. J. A. J. Meesters for his constructive comments. Natal Parks Board and University of Natal staff members willingly provided information and assistance. The Science Workshop made several pieces of equipment. Numerous field assistants enabled the successful completion of many lengthy and arduous tasks in the field. The Honourable Richard Emslie gave me access to his raw data from his research on the grazing ungulates of UGR. The CSIR, the University of Natal, and the University of Natal/Natal Parks Board Research Fund assisted financially.

Zusammenfassung

Die Auswirkungen von Überweidung auf Kleinsäuger im Umfolozi-Wildpark

Die Kleinsäugerpopulationen im Umfolozi-Wildpark in Südafrika wurden auf vier Probeflächen mit Fallengittern von Juli 1982 bis Dezember 1983 verfolgt. Verglichen wurden Savannen mit *Acacia nigrescens* und *A. tortilis* in Gebieten mit hoher Dichte großer Pflanzenfresser mit solchen Gebieten, in denen der Einfluß der Weidetiere auf die Hälfte reduziert war. In den weniger beweideten Gebieten waren Dichte und Diversität der Kleinsäuger höher als in den stark beweideten. Ferner war in den weniger beweideten Regionen der Anteil von Jungtieren höher und die durch Wiederfang geschätzte Lebenserwartung der Nager größer. Dagegen ergaben sich keine Nachweise für Unterschiede im Geschlechterverhältnis auf Flächen mit üppiger und spärlicher Vegetation bei den untersuchten Arten *Praomys natalensis, Saccostomus campestris* und *Aethomys chrysophilus.* Der mittlere Abstand mehrfach gefangener *Praomys natalensis* zwischen zwei Fängen war auf den stark beweideten Flächen größer. Bei *Saccostomus campestris* war ein derartiger Unterschied nicht nachweisbar. Die Trockenperiode von 1982/83 führte zu einem Abfall der Populationsdichte von Kleinsäugern im gesamten Untersuchungsgebiet.

Literature

Acocks, J. P. H. (1975): Veld types of South Africa. Mem. Bot. Survey of S.A. No. **40** 2nd ed.

Begon, M. (1979): Investigating Animal Abundance: capture-recapture for Biologists. London: Edward Arnold.

Bourquin, O.; Vincent, J.; Hitchins, P. M. (1971): The vertebrates of Hluhluwe Game Reserve-Corridor-Umfolozi Game Reserve Complex. The Lammergeyer **14,** 5–58.

Bransby, D. I.; Tainton, N. M. (1977): The Disc Pasture Meter: possible applications in grazing management. Proc. Grassld. Soc. Sth. Afr. **12,** 115–118.

Brooks, P. M. (1981): Population estimates and stocking rates of ungulates in U.G.R. and S. Corridor calculated for April, 1982 for use in the 1982–84 removal cycle. Unpubl. Natal Parks Board report, Pietermaritzburg.

De Graaff, G. (1981): The Rodents of Southern Africa. Pretoria: Butterworths.

Delany, M. J. (1964): An ecological study of the small mammals in the Queen Elizabeth Park, Uganda. Revue Zool. Bot. u.c.fr. **70,** 129–147.

— (1972): The ecology of small rodents in tropical Africa. Mamm. Rev. **2,** 1–42.

Emslie, R. H. (1982): The grazing impact of wild herbivores in Umfolozi Game Reserve. Unpubl.
French, N. R.; Grant, W. E.; Grodzinski, W.; Swift, D. M. (1976): Small mammal energetics in grassland ecosystems. Ecol. Monogr. **46,** 201–220.
Grant, W. E.; Birney, E. C. (1979): Small mammal community structure in North American grasslands. J. Mammology **60,** 23–36.
Grant, W. E.; Birney, E. C.; French, N. R.; Swift, D. M. (1982): Structure and productivity of small mammal communities related to grazing induced changes in vegetation cover. J. Mammalogy **63,** 248–260.
Hutcheson, K. (1970): A test for comparing diversities based on the Shannon formula. J. Theoret. Biol. **29,** 151–154.
Mc'Closkey, R. T. (1976): Community structure in sympatric rodents. Ecology **57,** 728–739.
McNaughton, S. J. (1976): Serengeti migratory wildebeest: facilitation of energy flow by grazing ungulates. Science **191,** 92–94
Sanders, E. H.; Gardner, P. D.; Berger, P. J.; Negus, N. C. (1981): 6-Methoxybenzoxazolinone: A plant derivative that stimulates reproduction in *Microtus montanus.* Science **214,** 67–69.
Shannon, C. E. (1948): A mathematical theory of communication. Bell System Tech. J. **27,** 379–423, 623–656.
Sokal, R. R.; Rohlf, F. J. (1981): Biometry. San Francisco: W. H. Freeman.
Willan, K. (1978): Design and field tests of a modified small mammal livetrap. S. Afr. J. Zool. **14,** 81–84.

Authors' address: A. E. Bowland and M. R. Perrin, Department of Zoology, University of Natal, PO Box 375, Pietermaritzburg 3200, South Africa

Z. Säugetierkunde 54 (1989) 261–264

ISSN 0044-3468

WISSENSCHAFTLICHE KURZMITTEILUNG

Ein weiterer subfossiler Fund der Sumpfspitzmaus (*Neomys anomalus* Cabrera, 1907) in Norddeutschland

Von D. Heinrich

Aus dem Institut für Haustierkunde der Universität Kiel

Eingang des Ms. 23. 2. 1989

Unter den wenigen Knochenresten, die bei der Ausgrabung einer spätmesolithischen, unmittelbar an der Trave gelegenen Siedlung (Ellerbek/Ertebølle; jüngeres Atlantikum, ca. 5000–6000 Bp) im südlichen Schleswig-Holstein (Schlamersdorf; nördlich von Bad Oldesloe) von S. Hartz, M. A., Archäologisches Landesmuseum der Universität Kiel, geborgen wurden, befand sich der aborale Teil eines Unterkiefers einer Spitzmaus (Abb. 1). Nach morphologischen Kriterien konnte das Fundstück der Gattung *Neomys* zugeordnet werden. Aufgrund des Maßes „Höhe des Ramus mandibulae" war eine genauere Determination möglich: Das Fundstück stammt von der Sumpfspitzmaus, *Neomys anomalus*. Mit einem Wert von 4,15 mm in diesem Maß liegt es nicht nur in dem für *Neomys anomalus* geltenden Variationsbereich, der bis 4,4 mm, im Höchstfall bei südöstlichen Populationen bis 4,5 mm oder gar bis 4,6 mm bei schweizerischen Sumpfspitzmäusen reicht (s. Zusammenstellung bei Pieper und Reichstein 1980), sondern auch unterhalb des für die Wasserspitzmaus, *Neomys fodiens*, ermittelten Minimalwertes. Da das Fundstück also eindeutig unterhalb des möglichen Überschneidungsbereiches zwischen beiden Arten liegt, der nach Bühler (1964a) Meßwerte zwischen 4,3 und 4,6 mm umfaßt, brauche ich hier nicht auf die vielfach erörterten Probleme der Differenzierung zwischen beiden Arten einzugehen (s. z. B. Pieper und Reichstein 1980).

Mit dem vorliegenden Fund ist ein dritter Nachweis der Sumpfspitzmaus für das



Abb. 1. Sumpfspitzmaus, *Neomys anomalus*. Aborales Fragment der rechten Mandibula, Ansicht von medial – Subfossilfund aus Schlamersdorf. Maßstab 10 : 1

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5404-0261 $ 02.50/0

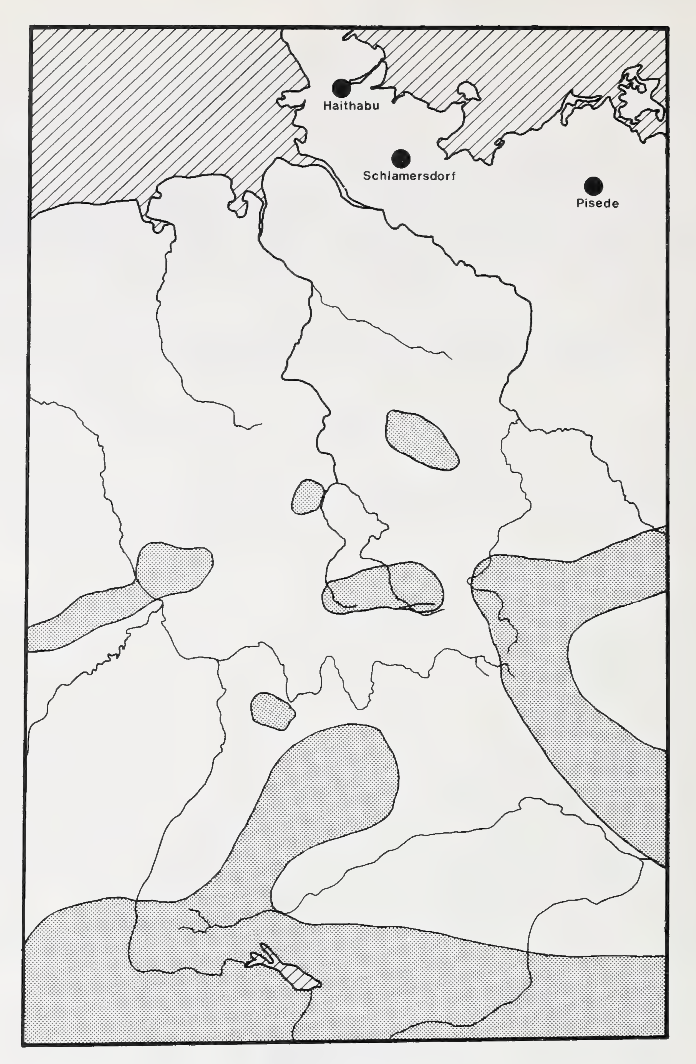


Abb. 2. Sumpfspitzmaus, *Neomys anomalus*. Fundorte subfossiler Reste und rezente Verbreitung in Anlehnung an ANGERMANN (1974) unter Berücksichtigung der Angaben von TENIUS (1953), VON LEHMANN (1963, 1972), BÜHLER (1964a, b), PIEPER (1966), VAN LAAR und DAAN (1976), GÖRNER (1977), VAN LAAR (1983) und HUTTERER (1984)

norddeutsche Tiefland erbracht worden, nachdem PIEPER und REICHSTEIN (1980) über einige Funde der Art aus Haithabu südlich von Schleswig berichtet haben und W.-D. HEINRICH (1983) sie im fossilen Tierbautensystem von Pisede bei Malchin in Mecklenburg nachweisen konnte (Abb. 2). Die zeitliche Einordnung dieser letztgenannten Funde ist schwierig; das Tierbautensystem wurde bereits im Spätglazial angelegt, die Funde der Sumpfspitzmaus ordnet W.-D. HEINRICH zusammen mit denen anderer temperater Arten etwa ins frühe bis mittlere Holozän. Die Reste aus Haithabu sind ins frühe Mittelalter, in den Zeitraum des 9.–11. Jahrhunderts n. Chr. zu stellen.

Diese Subfossilnachweise belegen, daß die Art nach dem Rückzug des Eises zunächst weit nach Norden vorgedrungen ist und später – offensichtlich frühestens vor ca. 1000

Jahren – wieder nach Süden zurückgedrängt wurde. Der neue Nachweis der Sumpfspitzmaus von Schlamersdorf macht durch seine Lage zwischen den beiden schon länger bekannten Fundorten wahrscheinlich, daß das ehemalige Verbreitungsgebiet kontinuierlich und umfangreich war. Das Ausmaß der Arealregression wird deutlich durch den großen Abstand dieser Fundorte vom nächsten rezenten Vorkommen der Art, dem Harz: Am nächstgelegenen, jedoch mehr als 200 km hiervon entfernt ist Schlamersdorf. Das heutige Areal ist gekennzeichnet durch eine weitgehende Aufsplitterung, insbesondere betrifft das den Bereich nördlich der Alpen. Man möchte diese Teilgebiete mit DE LATTIN (1967) zumindest teilweise als Reliktareale ansprechen (s. Abb. 2), obwohl auch nicht ausgeschlossen werden kann, daß für manche Gebiete bisher nur die Nachweise ausstehen (s. BÜHLER 1964a). Das konnte z. B. GÖRNER (1977) u. a. für den sächsischen Mittelgebirgsbereich zeigen.

Versucht man für die Regression des Areals der Sumpfspitzmaus eine Erklärung zu finden, so ist es hilfreich, die derzeitige Verbreitung zu berücksichtigen: Es fällt auf, daß innerhalb des von Spanien bis in die Ukraine und nach Kleinasien reichenden Gesamtareals (s. CORBET 1978; GÖRNER und HACKETHAL 1988) die verschiedenen Teilgebiete in West- und Mitteleuropa vorwiegend gebirgige Regionen, in Osteuropa aber auch Tiefländer umfassen. Darauf wurde bereits mehrfach hingewiesen (z. B. VON LEHMANN 1963; CORBET 1966). Die drei bekannten Fundorte subfossiler Reste der Art beweisen, daß in früherer Zeit auch die norddeutsche Tiefebene besiedelt war und es also keine Beschränkung auf Gebirgsregionen gab.

Es liegt nahe, für diese auf den Westteil der Gesamtverbreitung und dort auf das Tiefland begrenzte Regression nach Süden zumindest als einen wichtigen Faktor Klimaveränderungen verantwortlich zu machen. Wenn Temperatur und Feuchtigkeit seit der Wärmezeit (Boreal, Atlantikum) auch gewissen Schwankungen unterworfen waren, so ist das Klima in Norddeutschland insgesamt betrachtet doch kühler und auch feuchter geworden (s. hierzu OVERBECK 1975). In den südlich anschließenden Mittelgebirgen kamen diese Klimaveränderungen aufgrund anderer Höhenlage nicht so sehr oder in anderer Weise zur Geltung. Gleiches gilt für die weiter östlich liegenden Gebiete ganz allgemein, die klimatisch als kontinental einzustufen sind. Was im einzelnen ausschlaggebend gewesen sein mag für den Rückgang der Art auf im wesentlichen gebirgige Gebiete in West- und Mitteleuropa, muß offen bleiben. Vorstellbar ist z. B., daß die Schneebedekkung ein begrenzender Faktor ist: Im norddeutschen Flachland ist sie heute im Durchschnitt viel geringer als etwa in den Mittelgebirgen oder im östlichen Europa überhaupt.

Dem kleineren und disjunkten Areal von *Neomys anomalus* steht eine weite und kontinuierliche Verbreitung der Wasserspitzmaus *(Neomys fodiens)* über fast ganz Europa und weite Teile Sibiriens gegenüber (CORBET 1978). Das ist auffällig, denn mehrfach beobachtete syntope Vorkommen (s. VON LEHMANN 1963; VAN LAAR und DAAN 1976; NIETHAMMER 1977; VAN LAAR 1983) weisen auf ähnliche ökologische Ansprüche beider Arten hin. Nach SPITZENBERGER (1980) zeigt die Wasserspitzmaus jedoch eine größere Anpassungsfähigkeit an ihren Lebensraum als die Sumpfspitzmaus, so daß solche Unterschiede in der Biologie zwischen beiden Arten für die Differenzen in der Verbreitung mitverantwortlich sein könnten.

Literatur

ANGERMANN, R. (1974): Säugetiere – Mammalia. In: Exkursionsfauna, Wirbeltiere. Ed. by E. Stresemann. Berlin: Volk und Wissen.

BÜHLER, P. (1964a): Zur Gattungs- und Artbestimmung von *Neomys*-Schädeln – Gleichzeitig eine Einführung in die Methodik der optimalen Trennung zweier systematischer Einheiten mit Hilfe mehrerer Merkmale. Z. Säugetierkunde **29**, 65–93.

— (1964b): Zur Verbreitung und Ökologie der Sumpfspitzmaus (*Neomys anomalus milleri* Mottaz) in Württemberg. Veröff. Landesstelle f. Naturschutz u. Landschaftspflege Baden-Württemberg. **32**, 64–70.

Corbet, C. B. (1966): The Terrestrial Mammals of Western Europe. London: G. T. Foulis.
— (1978): The Mammals of the Palaearctic Region: a taxonomic review. London and Ithaca: British Museum (Natural History), Cornell University Press.
Görner, M. (1977): Weitere Nachweise der Sumpfspitzmaus *(Neomys anomalus)*, der Gartenspitzmaus *(Crocidura suaveolens)* und der Kleinäugigen Wühlmaus *(Pitymys subterraneus)* im Süden der DDR (Mammalia, Soricidae, Microtinae). Faun. Abh. Mus. Tierk. Dresden **6,** 219–224.
Görner, M.; Hackethal, H. (1988): Säugetiere Europas. Stuttgart: Ferdinand Enke.
Heinrich, W.-D. (1983): Untersuchungen an Skelettresten von Insectivoren (Insectivora, Mammalia) aus dem fossilen Tierbautensystem von Pisede bei Malchin. Teil 1, 2. Wissenschaftliche Zeitschrift der Humboldt-Universität zu Berlin. Mathematisch-naturwissenschaftliche Reihe **6,** 681–706.
Hutterer, R. (1984): Sumpfspitzmaus – *Neomys anomalus* Cabrera, 1907. In: Die Säugetiere Westfalens. Ed. by R. Schröpfer, R. Feldmann, H. Vierhaus. Münster: Abh. Westfäl. Mus. Naturkunde **46,** 68–69.
Laar, V. van (1983): A record of *Neomys anomalus* Cabrera, 1907 from the Vosges. Mammalia **47,** 123–125.
Laar, V. van; Daan, N. (1976): *Neomys anomalus* Cabrera, 1907, observé dans les Ardennes françaises. Lutra **18,** 44–51.
Lattin, G. de (1967): Grundriß der Zoogeographie. Stuttgart: Gustav Fischer.
Lehmann, E. von (1963): Die Säugetiere des Fürstentums Liechtenstein. Jb. Hist. Ver. Fürstentum Liechtenstein **62,** 159–362.
— (1972): Die Kleinsäugetiere des Naturparks „Rhein-Westerwald". Rheinische Heimatpflege N.F. **4,** 296–315.
Niethammer, J. (1977): Ein syntopes Vorkommen der Wasserspitzmäuse *Neomys fodiens* und *N. anomalus*. Z. Säugetierkunde **42,** 1–6.
Overbeck, F. (1975): Botanisch-geologische Moorkunde. Neumünster: Wachholtz.
Pieper, H. (1966): Über die Artbestimmung von *Neomys*-Mandibeln mit Hilfe der Fisherschen Diskriminanz-Analyse. Z. Säugetierkunde **31,** 402–403.
Pieper, H.; Reichstein, H. (1980): Zum frühgeschichtlichen Vorkommen der Sumpfspitzmaus (*Neomys anomalus* Cabrera, 1907) in Schleswig-Holstein. Z. Säugetierkunde **45,** 65–73.
Spitzenberger, F. (1980): Sumpf- und Wasserspitzmaus (*Neomys anomalus* Cabrera 1907 und *Neomys fodiens* Pennant 1771) in Österreich. Mitt. Abt. Zool. Landesmus. Joanneum **9,** 1–39.
Tenius, K. (1953): Bemerkungen zu den Säugetieren Niedersachsens. 2. Folge. Beitr. Naturkunde Niedersachsens **6,** 74–80.

Anschrift des Verfassers: Dr. Dirk Heinrich, Institut für Haustierkunde, Universität Kiel, Olshausenstr. 40, D-2300 Kiel

Subscription information for USA, Canada and Mexiko obtainable from Paul Parey Scientific Publishers/IR Unltd., 35 West 38th Street, Suite 3 W, New York, NY 10018, USA.

Erscheinungsweise und Bezugspreis 1989: 6 Hefte bilden einen Band. Jahresabonnement Inland: 318,– DM zuzüglich 13,80 DM Versandkosten, Gesamtpreis 331,80 DM einschließlich 7% Mehrwertsteuer. Jahresabonnement Ausland: 318,– DM zuzüglich 18,– DM Versandkosten. Das Abonnement wird zum Jahresanfang berechnet und zur Zahlung fällig. Es verlängert sich stillschweigend, wenn nicht spätestens am 15. November eine Abbestellung im Verlag vorliegt. Die Zeitschrift kann bei jeder Buchhandlung oder bei der Verlagsbuchhandlung Paul Parey, Spitalerstraße 12, D-2000 Hamburg 1, bestellt werden. Die Mitglieder der „Deutschen Gesellschaft für Säugetierkunde" erhalten die Zeitschrift unberechnet im Rahmen des Mitgliedsbeitrages.

Z. Säugetierkunde 54 (1989) 4, 193–264

Aus der Reihe:

Biologie und Evolution
interdisziplinär

Der Kreis um Konrad Lorenz
Ideen, Hypothesen, Ansichten

Herausgegeben von Prof. Dr. Wolfgang M. Schleidt, Wien, unter Mitwirkung zahlreicher Fachkollegen. 1988. 206 Seiten mit 6 Abbildungen. Gebunden DM 38,–
ISBN 3-489-63336-9

Durch den Tod von Konrad Lorenz wurde diese Sammlung von 47 Arbeiten, die seine Freunde und Schüler aus Anlaß seines 85. Geburtstages am 7. November 1988 zusammengetragen haben, zu einem Beitrag des Gedenkens, der Würdigung und des Dankes für ein großes Forscherleben.
Darüber hinaus ist dieses Buch ein wissenschaftsgeschichtliches Dokument der Entwicklung dieser Forschungsrichtung. Das Verzeichnis der etwa 500 im Text zitierten Veröffentlichungen umfaßt die wichtigsten Ergebnisse der Verhaltensforschung und enthält erstmals ein komplettes Werkverzeichnis von Konrad Lorenz.

Vom Werden zum Sein
Energetische und soziale Aspekte der Evolution

Von Univ.-Prof. Dr. Wolfgang Wieser, Innsbruck. 1989. Ca. 160 Seiten mit 17 Abbildungen und 8 Tabellen. Gebunden DM 38,– ISBN 3-489-64134-5

In der Geistesgeschichte der letzten Jahrhunderte wurde entweder die Dauer betont, die in der Aufeinanderfolge der Generationen wurzelt, oder die Dauer, die der Einzelne zu schaffen vermag. Einmal erscheint das Werden von Familien, von Völkern und Nationen von größerer Bedeutung, einmal das erfüllte Sein des Individuums.
Aus dieser Dialektik erwachsen Spannungen, die uns alle berühren. Die in diesem Buch zusammengefaßten Essays haben, auf verschiedene Weise, mit diesen Spannungen zu tun.

Kognitive, organische und gesellschaftliche Evolution

Von Dr.-Ing. Olaf Diettrich, Brüssel. 1989. Ca. 208 Seiten mit 12 Abbildungen. Gebunden DM 38,–
ISBN 3-489-64234-1

Der Autor beschreibt die Evolution als Prozeß fortschreitender Sozialisierung von den Einzellern über die mehrzelligen Lebewesen bis zu den sozialen und kulturellen Individualitäten. Die wesentlichen Parameter einer solchen Evolution sind die sich entwickelnden Theorien im weiteren Sinne wie organische und kognitive Fähigkeiten, mit denen sich Individuen in ihrer physischen bzw. sozialen Umwelt arrangieren. Auf der Grundlage dieses Theorienbegriffs skizziert der Autor die Elemente einer Theorie der Entwicklung von Theorien (TET), die die organische und kognitive Evolution ebenso einschließt wie die kulturelle und soziale.

Der Aufbau der Vernunft
Eine biologisch-philosophische Denkanleitung zur Mehrheitsfähigkeit der Vernunft

Von Prof. a. D. Dr. Fritz Preuß, St. Peter-Ording. 1989. Ca. 160 Seiten mit 2 Abbildungen. Kartoniert DM 28,–
ISBN 3-489-64434-4

Die Unterscheidung und gegenseitige Zuordnung von Vernunft und Verstand war die für die menschliche Zukunft ermutigendste Erkenntnis seiner neuen Evolutionstheorie, mit der Fritz Preuß die Entwicklung der Lebewesen bis zum „Aufbau des Menschlichen" erklärt. In seinem so betitelten, 1987 erschienenen Buch wurde bereits das Vernunfterleben der Seele angesprochen. Sein neues Buch gilt der Weiterführung der dort entwickelten Gedanken und Theorien. Neben der Vertiefung der Herkunft und des Aufbaus dieses Vernunfterlebens wird dessen entscheidender Anteil beim Aufbau der Zukunft menschlichen Lebens deutlich gemacht.

Sozialisation und Ontogenese

Von Dr. Detlef W. Promp, Wildeshausen. 1989. Ca. 208 Seiten mit 14 Abbildungen. Gebunden DM 38,–
ISBN 3-489-64334-8

Es ist in der Sozialisationsforschung üblich, im Menschen ein Lebewesen zu sehen, das primär durch seine soziokulturelle Umwelt geformt wird. Dem stammesgeschichtlich Erworbenen wird dabei oft nur eine untergeordnete Rolle gegenüber dem zu Lernenden zugestanden. In dieser Arbeit wird nun versucht, das Verhältnis von phylogenetischer Vorgabe und soziokulturellen Lernangeboten und -notwendigkeiten näher zu bestimmen, wobei als Voraussetzung für das Verständnis der Darstellung der biologischen Grundlagen des menschlichen Verhaltens breiter Raum gegeben wird.

Fordern Sie unseren kostenlosen Sammelprospekt *„Biologie und Evolution interdisziplinär"* an.

Preise: Stand 1. 4. 1989



Berlin
und
Hamburg

Vol. 54 (5), 265–336, Oktober 1989 ISSN 0044-3468 C 21274 F

ZEITSCHRIFT FÜR SÄUGETIERKUNDE

INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde



Verlag Paul Parey Hamburg und Berlin

This journal is covered by Biosciences Information Service of Biological Abstracts, and by Current Contents (Series Agriculture, Biology, and Environmental Sciences) of Institute for Scientific Information

---

Die Zeitschrift für Säugetierkunde veröffentlicht Originalarbeiten und wissenschaftliche Kurzmitteilungen aus dem Gesamtgebiet der Säugetierkunde, Besprechungen der wichtigsten internationalen Literatur sowie die Bekanntmachungen der Deutschen Gesellschaft für Säugetierkunde. Verantwortlicher Schriftleiter im Sinne des Hamburgischen Pressegesetzes ist Prof. Dr. Harald Schliemann.

Zusätzlich erscheint einmal im Jahr ein Heft mit den Abstracts der Vorträge, die auf der jeweiligen Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde gehalten werden. Sie werden als Supplement dem betreffenden Jahrgang der Zeitschrift zugeordnet. Verantwortlich für ihren Inhalt sind ausschließlich die Autoren der Abstracts.

Manuskripte: Manuskriptsendungen sind zu richten an die Schriftleitung, z. Hd. Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Biologie-Zentrum, Neue Universität, Olshausenstr. 40–60, D-2300 Kiel. Für die Publikation vorgesehene Manuskripte sollen gemäß den „Redaktionellen Richtlinien" abgefaßt werden. In ihnen finden sich weitere Hinweise zur Annahme von Manuskripten, Bedingungen für die Veröffentlichung und die Drucklegung, ferner Richtlinien für die Abfassung eines Abstracts und eine Korrekturzeichentabelle. Die Richtlinien sind auf Anfrage bei der Schriftleitung und dem Verlag erhältlich.

Sonderdrucke: Anstelle einer Unkostenvergütung erhalten die Verfasser von Originalbeiträgen und Wissenschaftlichen Kurzmitteilungen 50 unberechnete Sonderdrucke. Mehrbedarf steht gegen Berechnung zur Verfügung, jedoch muß die Bestellung spätestens mit der Rücksendung der Korrekturfahnen erfolgen.

Mit einer Beilage des Verlages Paul Parey

Fortsetzung 3. Umschlagseite

© 1989 Paul Parey. Verlag: Paul Parey, Hamburg und Berlin. Anschriften: Spitalerstr. 12, D-2000 Hamburg 1; Lindenstr. 44–47, D-1000 Berlin 61. – Printed in Germany by Westholsteinische Verlagsdruckerei Boyens & Co., D-2240 Heide/Holst.

Z. Säugetierkunde 54 (1989) 265–275

ISSN 0044-3468

Muzzle rubbing in the moustached tamarin, *Saguinus mystax* (Primates: Callitrichidae) – behavioural and histological aspects

By E. W. Heymann, U. Zeller and M. H. Schwibbe

Deutsches Primatenzentrum, Göttingen and Abteilung Morphologie, Zentrum Anatomie der Universität Göttingen

Receipt of Ms. 27. 1. 1988

Abstract

Muzzle rubbing (rubbing of the oro-nasal region against the substrate) was studied in a pair of moustached tamarins, *Saguinus mystax mystax,* in an outdoor enclosure. Muzzle rubbing was frequently associated temporally and spatially with anogenital and suprapubical marking and urination. Specialized mono- and polyptychic skin glands were found above the anterior nasal cupula and in the surrounding skin. From this evidence and the comparison with other primates the hypothesis is developed that muzzle rubbing is envolved in scent marking. In the female moustached tamarin, longterm cyclic changes in frequencies of muzzle rubbing were found which are possibly related to the oestrous cycle. Therefore, it is suggested that muzzle rubbing plays a role in the communication of the reproductive status of the female.

Introduction

Communication by chemical signals plays an important role in the social and reproductive behaviour of primates (Epple 1986). Among the New World monkeys, in marmosets and tamarins (Callitrichidae) secretions from scent gland organs in the circumgenital and sternal regions, and urine are suggested to be the main carriers of olfactory informations (Epple 1974, 1978; Zeller et al. 1988). They are deposited at the environment by means of scent-marking behaviours like anogenital, suprapubical and sternal marking. These behaviour patterns have been observed in all callitrichids studied so far (Epple 1986; Heymann 1985).

Many species of callitrichids and some other primates frequently rub their muzzle against the substrate (Table 1). This behaviour is interpreted by French and Cleveland (1984) as scent-marking, whereas Sutcliffe and Poole (1978, p. 53) argue that "the absence of glandular fields militates against muzzle rubbing being a form of scent marking". However, in callitrichids, the histology of the skin of the muzzle, viz. in the area above the anterior nasal cupula, has never been studied in detail. Among the primates listed in Table 1, only in *Tarsius* specialized circumoral skin glands ("Zirkumoralorgan") have been described by Sprankel (1971).

In addition to the lack of studies dealing with the microscopical anatomy of the skin of the muzzle, little behavioural data on frequencies, contexts, temporal and spatial patterning of muzzle rubbing have been presented. Sex-specific differences in frequencies of muzzle rubbing have been reported for howler monkeys *(Alouatta seniculus)* where it is mainly performed by males (Braza et al. 1981). In contrast, no sexual dimorphism in frequencies of muzzle rubbing is observed in the cotton-top tamarins *(Saguinus oedipus)* and in a mixed pair of saki monkeys (*Pithecia hirsuta* and *Pithecia monachus*) muzzle rubbing occurred with equal frequencies in both sexes (French and Cleveland 1984; Bartecki and Heymann 1987). In Goeldi's tamarin *(Callimico goeldii)* and in lesser mouse lemurs *(Microcebus murinus)* muzzle rubbing occurs more frequently in females during the oestrous (Glatston 1983; Heltne et al. 1981).

In the present paper the muzzle rubbing behaviour of the moustached tamarin

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5405-0265 $ 02.50/0

Table 1. **Muzzle rubbing and comparable behaviour patterns in callitrichids and other primates**

Species	Behaviour pattern	Reference
Callithrix jacchus	muzzle rub	STEVENSON and POOLE 1976; SUTCLIFFE and POOLE 1978
Callithrix argentata	muzzle rub	OMEDES 1981
Saguinus labiatus labiatus	muzzle rub	COATES and POOLE 1983
Saguinus mystax mystax	muzzle rubbing	HEYMANN 1985
Saguinus fuscicollis nigrifrons	muzzle rubbing	HEYMANN 1985
Saguinus oedipus	nose rubbing	FRENCH AND CLEVELAND 1984
Saguinus geoffroyi	face rubbing	MOYNIHAN 1970
Callimico goeldii	nose-rub marking, nose-rub grooming, sneeze-nose rub	HELTNE et al. 1981
Saimiri sciureus	nasal rubbing	SCHWARTZ and ROSENBLUM 1980
Pithecia pithecia	naso-buccal rubbing	DUGMORE 1986
Pithecia hirsuta	muzzle rubbing	BARTECKI and HEYMANN 1987
Pithecia monachus	muzzle rubbing	BARTECKI and HEYMANN 1987
Alouatta seniculus	muzzle rubbing	BRAZA et al. 1981
Tarsius bancanus borneanus	head rubbing	SPRANKEL 1971
Tarsius syrichta carbonarius	head rubbing	SPRANKEL 1971
Microcebus murinus murinus	mouth wiping	GLATSTON 1983
Galago demidovii demidovii	mouth rubbing, labial marking	VOLAND 1978

(Saguinus m. mystax) is analysed and histological evidence in favour of the scent marking hypothesis is reported.

Material and methods

A pair of wildborn moustached tamarins (*Saguinus mystax mystax* Spix, 1823) living in a $9 \times 13 \times 2.5$ m outdoor enclosure at the Centro de Reproducción y Conservación de Primates (CRCP) in Iquitos (Peru) was observed by one of us (EWH) during the course of a study on vocal and olfactory communication (HEYMANN 1985). The outdoor enclosure was equipped with natural plant growth and a system of wooden perches. It contained two small cages in which food was placed twice daily and water was available ad libitum. For further details on the enclosure see KAUMANNS (1982). Between October 16, 1982 and March 27, 1983, 252 hours of observation focussing on olfactory behaviour were carried out. Together with records on scent-marking, sniffing, licking and other behaviours related to olfactory communication, all observed events of muzzle rubbing were recorded, stating animal, time, context and spatial position. Ambient temperature was read every 15 min during observation sessions from a maximum-minimum-thermometer placed near the observer's seat at the front side of the enclosure.

Statistical procedures

Individual rates and diurnal variation in frequencies of muzzle rubbing were calculated by the two-way analysis of variance and covariance (ANOVA). Frequencies are given per 15 min (total number of 15-min periods: 1007). Spatial frequency distributions were compared with the χ^2-test. Long-term changes in frequencies of muzzle rubbing were determined with the analysis of autocorrelation. In this analysis, observed values at time t are successively correlated with the values at t+1, t+2, . . . , t+n (time lag). The correlation coefficients are then plotted as a function of the time lag. Thus, periodical variations can be detected and the period length can be determined (for further details see LIENERT 1978).

Histological methods

The circumoral skin together with the anterior end of the cartilaginous nasal skeleton (Cupula nasi anterior) of an adult male *Saguinus m. mystax* were excised soon after natural death and fixed in 80 % ethanol at the CRCP in Iquitos. The material was embedded in paraffin, sectioned serially at 12 μm and stained with Hematoxyline-Eosine (H.E.) and Goldner's trichrome at the Zentrum Anatomie, University of Göttingen.

Serial sections of the skin covering the anterior nasal cupula of *Saguinus fuscicollis* and *Saguinus oedipus* were available for comparison.

Results

Description and behavioural context of muzzle rubbing

Muzzle rubbing consists of pressing the oro-facial region onto the substrate and rubbing it with lateral movements of the head (Fig. 1). It is always performed on horizontal or slightly inclined substrates.



Fig. 1. Muzzle rubbing in a male moustached tamarin, *Saguinus mystax mystax*

Muzzle rubbing has been observed to occur in the following behavioural contexts: a. before or during scent marking and urination; b. after feeding; c. before or after sneezing; d. without definable context.

Contexts (a) and (b) occasionally were combined, i.e. the animals muzzle rubbed after feeding and before or during scent marking and urination. The movement patterns were essentially the same in all situations. Table 2 shows the relative frequencies of muzzle rubbing in the forementioned contexts. Clear differences between male and female only exist in the frequency of muzzle rubbing after feeding and before or during scent marking and urination and muzzle rubbing that was observed without definable context.

Individual frequencies and diurnal distribution of muzzle rubbing

Muzzle rubbing was observed totally 602 times, 295 times in the male and 287 times in the female. Average frequency per 15 min was 0.29 ($\pm$ 0.71) for the male and 0.28 ($\pm$ 0.61) for the female; the difference is not statistically significant (ANOVA: $F = 0.13$, $df = 1, 1990$, $p = 0.71$).

Frequencies of muzzle rubbing show significant variation during the day (ANOVA: $F = 8.18$, $df = 11, 1990$, $p = 0.000$; Fig. 2). In both animals a pronounced maximum is present in the early morning, but frequencies vary only slightly during the rest of the day.

Table 2. **Behavioural contexts of muzzle rubbing in *Saguinus mystax***
Figures indicate the percentage of muzzle rubbing that was observed within each context

	Male	Female
After feeding	16.3	17.8
Before or during scent marking and urination	29.2	34.8
After feeding and before or during scent marking and urination	1.4	10.5
Before or after sneezing	1.0	1.7
No definable context	52.2	35.2

There is no interaction between individual and time of day (F = 1.43, df = 11, 1990, $p = 0.15$). This is because the temporal distributions of male and female are essentially similar except for a significant difference between 1400–1500 h (T-Test: t = −2.21, df = 206, $p < 0.03$).

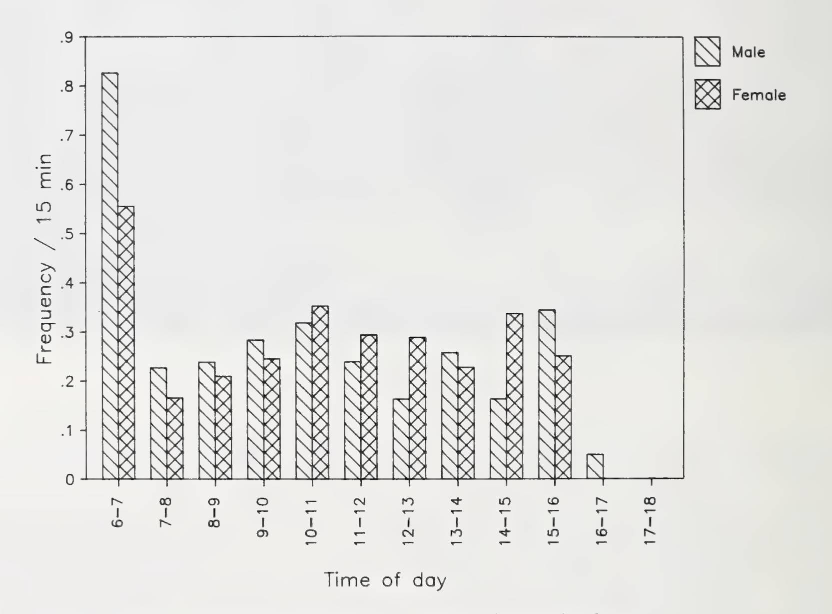


Fig. 2. Temporal distribution of muzzle rubbing during the day

Ambient temperature as a possible covariate has no influence on frequencies of muzzle rubbing (ANOVA: F = 0.01, df = 1, 1990, $p = 0.94$).

Spatial distribution of muzzle rubbing

The spatial distribution of muzzle rubbing within the outdoor enclosure is shown in Fig. 3. Both distributions are significantly different from a random distribution (male: χ^2 = 103.314, df = 19, $p < 0.001$; female: χ^2 = 88.378, df = 19; $p < 0.001$) and significantly different from each other (χ^2 = 60.253, df = 19, $p < 0.001$). The spatial distribution of muzzle rubbing of the male is significantly correlated with the distribution of its anogenital

marking ($r = 0.51$, $df = 18$, $p < 0.025$), but not with the distribution of the female's anogenital marking. The spatial distribution of the female's muzzle rubbing also is significantly correlated with its own anogenital marking ($r = 0.77$, $df = 18$, $p < 0.001$), but not with the male's anogenital marking. The stronger correlation for the female is a consequence of the more frequent association of muzzle rubbing with scent marking than in the male.

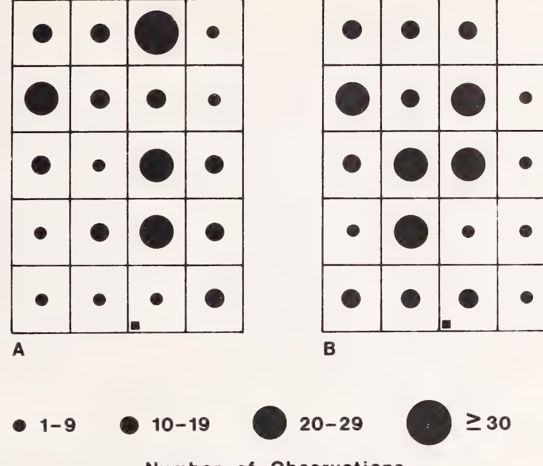


Fig. 3. Spatial distribution of muzzle rubbing in the outdoor enclosure. A: male, B: female; ■ observer's seat)

Long-term changes in frequencies of muzzle rubbing

The time period analyzed comprised 107 days from December 2, 1982 to March 18, 1983. For this period data are available for nearly every day; ten lacking values were substituted by random values lying within the range of variation of the total sample. Since an influence of time of day on frequencies of muzzle rubbing was found (see above) values had to be corrected for this.

Figure 4 shows the long-term changes in frequencies of muzzle rubbing. Whilst the male exhibits irregular fluctuations, a more regular pattern is present in the female.

An analysis of autocorrelation was performed to reveal the significance of the cyclicity. From Fig. 5a it can be seen that no cyclicity is present in the male. In the female a significant correlation is found at a half cycle length of 8 to 9 days ($r = -0.255$, $df = 97$, $p < 0.01$) and at a full cycle length of 17 to 18 days ($r = 0.156$, $df = 89$, $p < 0.1$) (Fig. 5b), which refers well to the interpeak intervalls indicated in Fig. 4b.

Histological findings

As in all platyrrhines, the width of the internarial space of *S. mystax* corresponds to that of the large Cartilago cupularis which forms the anterior boundary of the nasal cavity and, in addition to the Processus lateralis ventralis, is the main part of the anterior nasal cupula. The skin above the Cartilago cupularis is moderately covered with hair. Vibrissae are sporadically found. The Epidermis consists of approximately 5–7 cell layers: the cornified layer is relatively thick. The Dermis is made up of fibrous collaganous connective tissue and is extensively supplied by blood vessels. It is connected to the Perichondrium of the Cartilago cupularis; the Subcutis is lacking in this area.

Lateral to the anterior nasal cupula bundles of smooth muscle cells of the mimic musculature extend into the Subcutis and Dermis. Mono- and polyptychic skin glands are well developed in the skin above the Cupula nasi anterior (Fig. 6). The polyptychic or sebaceous glands have an alveolar structure. Numerous lobules empty into the upper third of the hair follicle. The ducts are short and wide; their walls are formed of several layers of cells. The lobules of the polyptychic glands are larger and their ducts have a wider lumen compared to those of unspecialized areas of the skin, e.g. the skin of the thigh.

The monoptychic apocrine glands have a tubular structure. They are more numerous and larger than in unspecialized areas of the skin. The apocrine glands are situated in a

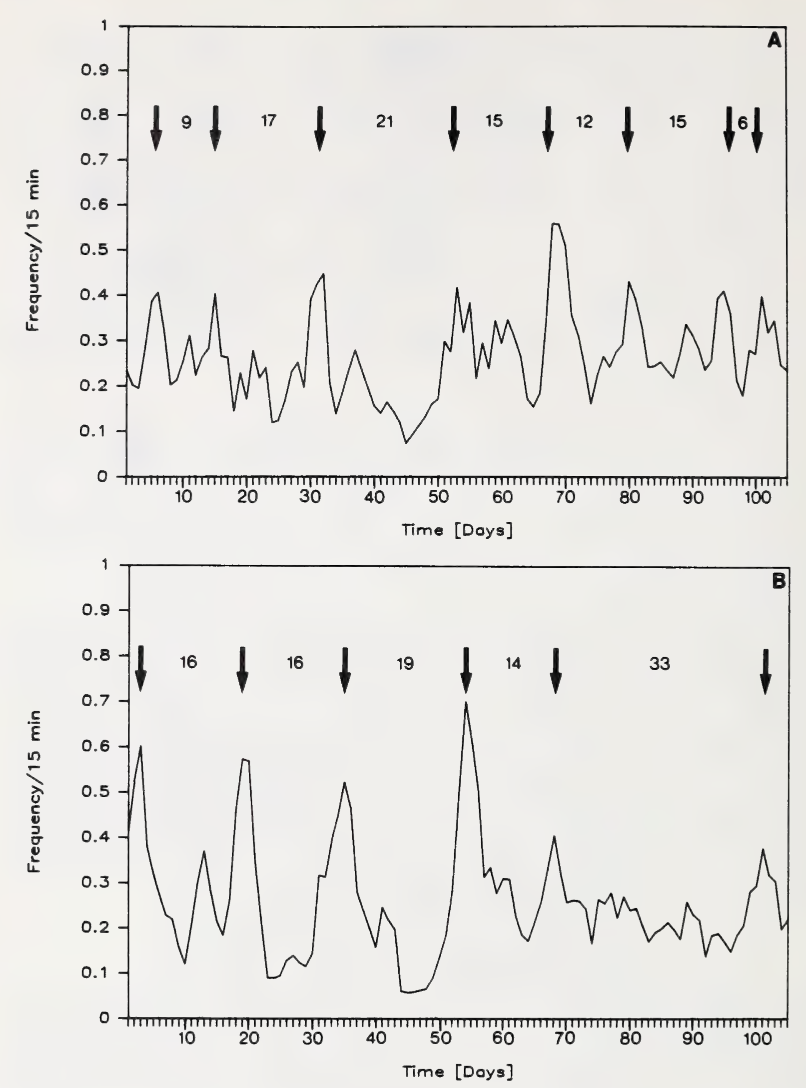


Fig. 4. Long-term changes in frequencies of muzzle rubbing (moving average, N = 3). A: Male, B: Female. Figures between arrows indicate the number of days between subsequent frequency peaks

deeper layer of the dermis below the sebaceous glands. The excreting ducts are elongated and have a narrow lumen; their wall consists of two layers of flattened cells. They closely adjoin the hair follicles and open into the distal, funnelshaped portion of the follicle. The monoptychic tubules form small groups within the connective tissue of the Dermis. Lateral to the anterior nasal cupula they extend into the subcutaneous layer. In segments of the tubules with a wide lumen, the secreting cells are flattened. In those segments with a narrow lumen, the epithelial cells are tall columnar and obviously in the process of secretion.

The mono- and polyptychic glands of the skin adjacent to the anterior nasal cupula are also larger than in unspecialized areas but their number and size rapidly decrease in the lateral direction.

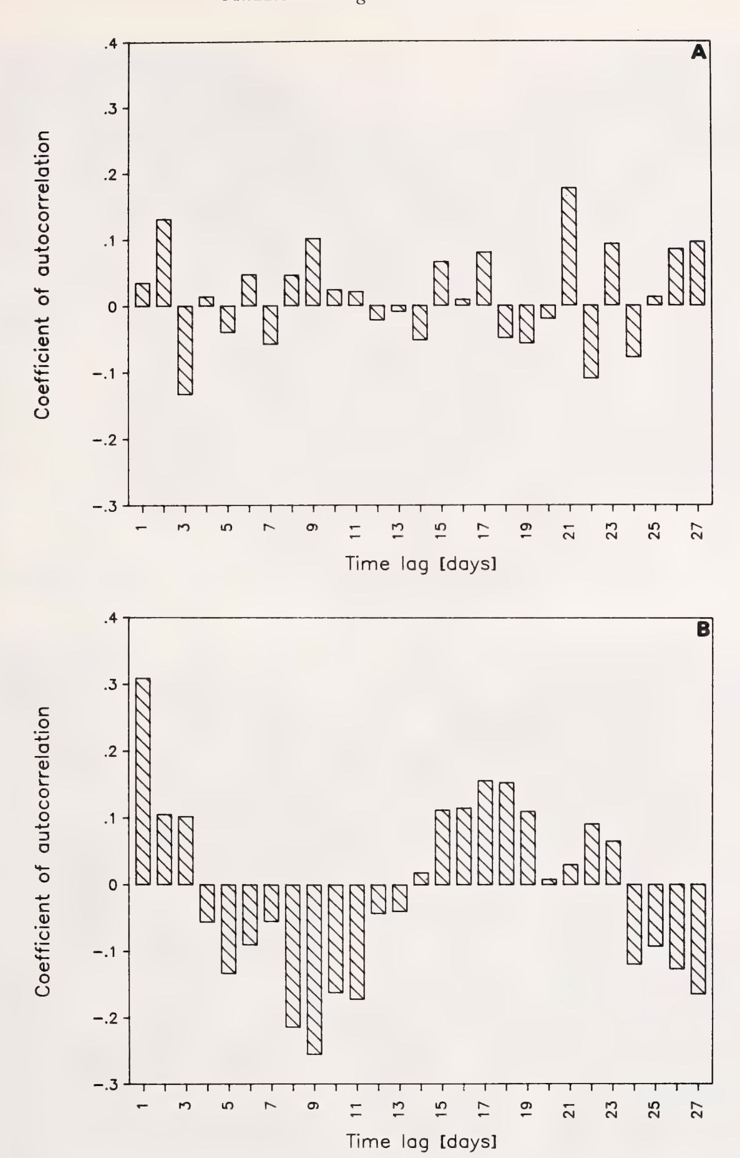


Fig. 5. Coefficients of autocorrelation for long-term changes in frequencies of muzzle rubbing. A: Male, B: Female

In *Saguinus fuscicollis,* the skin glands above the anterior nasal cupula are developed to a similar degree as in *S. mystax*. In *Saguinus oedipus,* however, they are smaller and less numerous than in *S. mystax* and *S. fuscicollis.*

Discussion

The behavioural and histological evidence presented in this study suggests that in the moustached tamarin *(S. mystax)* muzzle rubbing is involved in chemical communication.

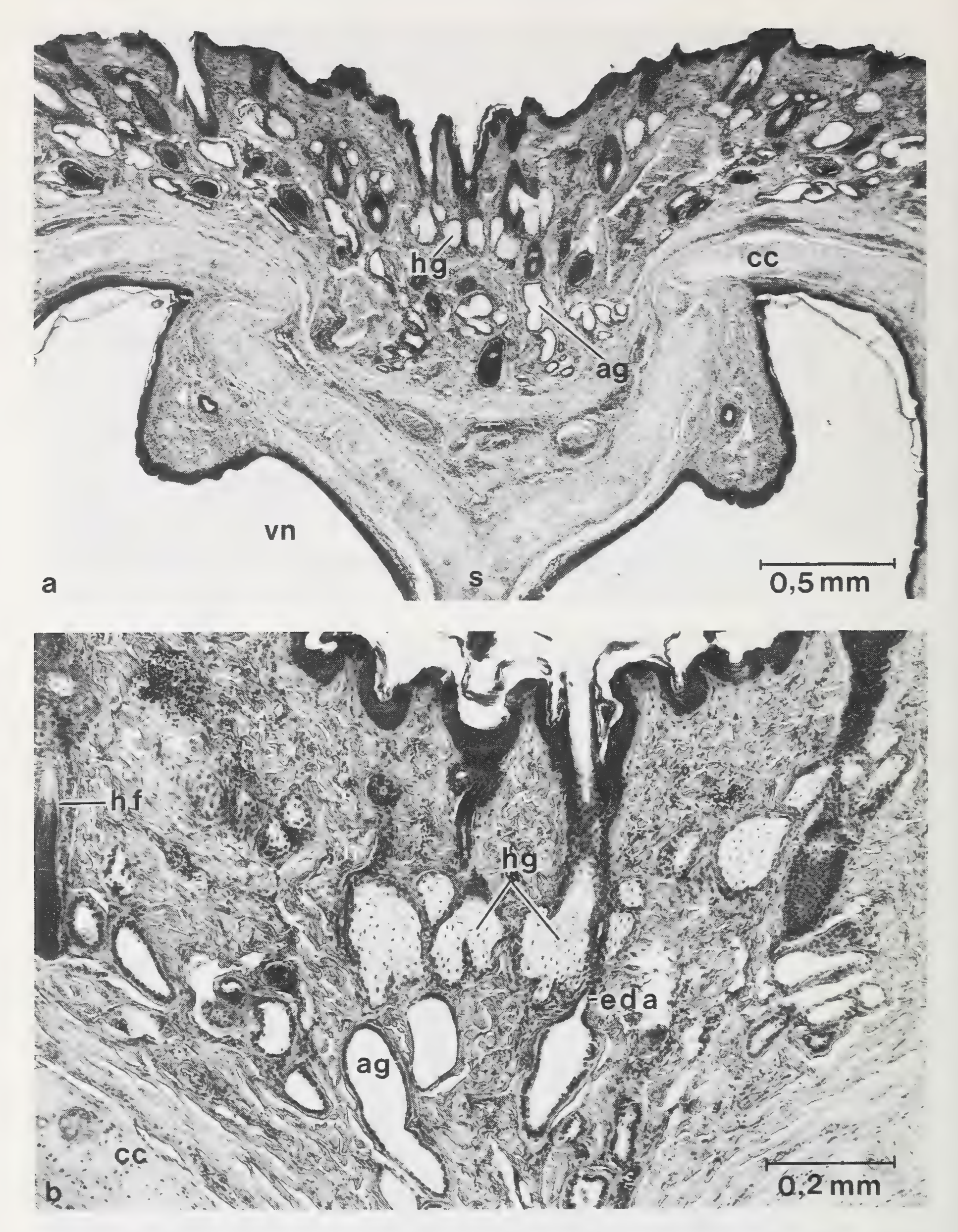


Fig. 6. Saguinus mystax mystax ♂, transverse sections through the nose at the anterior nasal cupula. Note the presence of specialized monoptychic (apocrine) and polyptychic (holorine) skin glands. ag = apocrine gland; cc = Cartilago cupularis; eda = excretory duct of apocrine gland; hf = hair follice; hg = holocrine gland; s = nasal septum; vn = Vestibulum nasi

This is shown by the frequent temporal and spatial association of muzzle rubbing with anogenital and suprapubical scent marking and urination. In addition, specialized mono- and polyptychic skin glands are found in the area above the anterior nasal cupula and the surrounding skin. This part of the face intensively contacts the substrate during muzzle rubbing (Fig. 1).

A temporal association of muzzle rubbing with scent marking has also been observed in *Saguinus labiatus* (Coates and Poole 1983), *Saguinus geoffroyi* (Moynihan 1970) and *Saguinus fuscicollis* (Heymann pers. obs.). In the latter, muzzle rubbing occurs with similar frequencies and in the same contexts as in *S. mystax*. There is no significant difference in the development of the skin glands of the face in these two species. In contrast, *Saguinus oedipus* possesses less and smaller skin glands on the external nose than *S. mystax* and *S. fuscicollis*. Large sebaceous glands have been found only in the lips of this species by Perkins (1969a). The behavioural findings are inconsistent: while French and Cleveland (1984) found high frequencies of muzzle rubbing, it was only seldom observed by Rohrhuber (pers. comm.) during her long-term study on the behaviour of *S. oedipus*. Generally, scent glands are less developed in this species compared to *S. fuscicollis* and are also smaller in the anogenital region (Zeller et al. 1988, in press). Large sebaceous glands are also found in the skin of lips and nose in *Callithrix argentata* (Perkins 1969c), and of lips, nose and cheeks in *Callimico goeldii* (Perkins 1969b). Muzzle rubbing has been described in both species. Quantitative behavioural and histological data are lacking for other platyrrhines.

Among other primates, only in *Tarsius bancanus* and *Tarsius syrichta* large polyptychic (holocrine) and monoptychic (apocrine) skin glands have been found in the upper and lower lips ("Zirkumoralorgan") by Sprankel (1971). Secretions of these glands are deposited by rubbing the face against the substrate, similar to muzzle rubbing of *Saguinus*. Besides, in *Tarsius* and *Saguinus* rubbing of the muzzle also occurs in connection with feeding or sneezing. This suggests that it also functions as a comfort behaviour, that is cleaning of the oro-nasal region, as it is also observed in some Cercopithecidae.

The occurrence of specialized skin glands in the oro-nasal region indicates that during muzzle rubbing secretions (and possibly saliva) can be released and deposited at the environment. Therefore, it is concluded that muzzle rubbing plays a role in scent marking. In addition, the presence of a functioning vomeronasal organ in platyrrhines (Maier 1980) suggests that muzzle rubbing is also involved in the perception of chemical signals. Belcher et al. (in press) demonstrated that close contact of the external nose to the substrate is a prerequisite for the discrimination of scent marks in *S. oedipus*.

The functions of chemical signals encoded in secretions of skin glands of the oro-nasal region are still unknown. However, the long-term cyclic fluctuations in frequencies of muzzle rubbing in a female *S. mystax* suggest that information on the reproductive status (e.g. oestrous) of the female can be released. The average length of the oestrous cycle is not exactly known for *S. mystax*. In the closely related *S. fuscicollis* average cycle lengths of 17.5 days (Epple and Katz 1984) and 14.6 days (Hampton and Hampton 1977) have been observed. For *S. oedipus* 15.2 days (Hampton and Hampton 1977), 15.5 days (Preslock et al. 1973), and 22.7 days (Brand 1981) are found. The data presented here for *S. mystax* are suggestive: the intervals between peaks in frequencies of muzzle rubbing in the female (except the last one) lie within the range of oestrous cycle length in related species. Additional support for the hypothesis that muzzle rubbing plays a role in the communication of the reproductive status of the female is lent by the observation of increased frequencies of muzzle rubbing during oestrus in female *Callimico goeldii* (Heltne et al. 1981) and in female *Microcebus murinus* (Glatston 1983).

Future studies on the social and reproductive behaviour of *Saguinus mystax* and other callitrichids will further elucidate the biological importance of muzzle rubbing.

Zusammenfassung

Reiben der oro-nasalen Region beim Schnurrbarttamarin, Saguinus mystax (Primates: Callitrichidae)

Reiben der Mund-Nasen-Region am Substrat wurde bei einem Paar von Schnurrbarttamarinen *(Saguinus mystax mystax)* in einem Freigehege untersucht. Dieses Reiben war häufig zeitlich und räumlich mit anogenitalem und suprapubischem Markieren und Urinieren assoziiert. Spezialisierte mono- und polyptyche Drüsen wurden in der Haut über der vorderen Nasenkuppel und im unmittelbar angrenzenden Bereich nachgewiesen. Diese Befunde deuten darauf hin, daß das Reiben der oro-nasalen Region bei *Saguinus mystax* dem Funktionskreis der olfaktorischen Kommunikation zuzuordnen ist. Beim Weibchen wurden langfristige zyklische Häufigkeitsschwankungen des Reibens festgestellt, die einen Zusammenhang mit dem Östruszyklus vermuten lassen. Möglicherweise dient diese Verhaltensweise auch der Kommunikation des Reproduktionszustandes des Weibchens.

Resumen

Frotar la boca en el pichico de barba blanca, Saguinus mystax (Primates: Callitrichidae) – aspectos etológicos e histológicos

Frotar la boca sobre el substrato fue observado en una pareja de pichicos de barba blanca *(Saguinus mystax mystax)* en un galpón al aire libre. Este comportamiento estuvo asociado temporalmente y espacialmente con marcaciones olfatorias y urinación. Glandulas mono- y poliptijas especializadas fueron encontradas en la Cupula nasi anterior y en la piel circundante. Estos resultados indican que frotar la boca en pichicos de barba blanca forma parte de la comunicación olfatoria. En la hembra, fluctuaciones a largo plazo de las frecuencias de frotar la boca fueron observadas, lo que indica posiblemente una correlación con el ciclo de estro. Posiblemente, con este comportamiento la hembra dé informaciones sobre su estado de reproducción.

Acknowledgements

This paper is based in part on a doctoral thesis of E. W. Heymann, supported by a grant from the Deutsches Primatenzentrum. We thank the Proyecto Primates in Iquitos for permission to study the moustached tamarins at the Centro de Reproducción y Conservación de Primates and for providing the material of *Saguinus mystax*. We would like to thank Mrs. Jutta Zeller for preparation of the serial sections and the help with the photographic work. EWH is deeply indepted to Dr. Jaime Moro S., Dr. Carlos Malaga and Luis Sicchar V. for their friendly help.

References

Bartecki, U.; Heymann, E. W. (1987): Über Schweifaffen in Peru. Z. Kölner Zoo **30**, 79–92.

Belcher, A.; Epple, G.; Küderling, I.; Smith, A. B., III. (1988): The volatile components of scent material from the cotton-top tamarin *(Saguinus o. oedipus):* a chemical and behavioral study. J. chem. Ecol. (in press).

Brand, H. M. (1981): Urinary estrogen excretion in the female cotton-topped tamarin *(Saguinus oedipus oedipus).* J. Reprod. Fertil. **62**, 467–473.

Braza, F.; Alvarez, F.; Azcarate, T. (1981): Behaviour of the red howler monkey *(Alouatta seniculus)* in the Llanos of Venezuela. Primates **22**, 459–473.

Coates, A.; Poole, T. B. (1983): The behaviour of the callitrichid monkey, *Saguinus labiatus labiatus,* in the laboratory. Int. J. Primatol. **4**, 339–371.

Dugmore, S. (1986): Behavioural observations on a pair of captive white-faced saki monkeys *(Pithecia pithecia).* Folia primatol. **46**, 83–90.

Epple, G. (1974): Pheromones in primate reproductive behaviour. In: Reproductive behaviour. Ed. by W. Montagna and W. A. Sadler. New York, London: Plenum Press, pp. 131–155.

— (1978): Studies on the nature of chemical signals in scent marks and urine of *Saguinus fuscicollis* (Callitricidae, Primates). J. chem. Ecol. **4**, 383–394.

— (1986): Communication by chemical signals. In: Comparative Primate Biology, vol. 2, part A: Behavior, Conservation, and Ecology. Ed. by G. Mitchell and J. Erwin. New York: Alan R. Liss, pp. 531–580.

Epple, G.; Katz, Y. (1984): Social influences on estrogen excretion and ovarian cyclicity in saddle back tamarins *(Saguinus fuscicollis).* Am. J. Primatol. **6**, 215–227.

French, J. A.; Cleveland, J. (1984): Scent-marking in the tamarin, *Saguinus oedipus:* sex differences and ontogeny. Anim. Behav. **32**, 615–623.

Glatston, A. R. (1983): Olfactory communication in the lesser mouse lemur *(Microcebus murinus).*

In: Perspectives in Primate Biology. Ed. by P. K. Seth. New Delhi: Today & Tomorrow's Printers and Publishers. pp. 63–73.

HAMPTON, S. K.; HAMPTON, J. K., Jr. (1977): Detection of reproductive cycles and pregnancy in tamarins (*Saguinus* spp.). In: The Biology and Conservation of Callitrichidae. Ed. by D. G. Kleiman. Washington: Smithsonian Institution Press, pp. 173–179.

HELTNE, P. G.; WOJCIK, J. F.; POOK, A. G. (1981): Geoldi's monkey, genus *Callimico*. In: Ecology and Behavior of Neotropical Primates. Ed. by A. F. Coimbra-Filho and R. A. Mittermeier. Rio de Janeiro: Academia Brasileira de Ciências, Vol. **1**, 169–209.

HEYMANN, E. W. (1985): Untersuchungen zur vokalen und olfaktorischen Kommunikation des Schnurrbarttamarins, *Saguinus mystax mystax* (Spix, 1823) (Primates: Callitrichidae). Doctoral Diss. University of Gießen.

KAUMANNS, W. (1982): Verhaltensbeobachtungen an Schnurrbarttamarinen *(Saguinus m. mystax)*. Z. Kölner Zoo **25**, 107–117.

LIENERT, G. A. (1978): Verteilungsfreie Methoden in der Biostatistik, Vol. 2. Meisenheim am Glan: Verlag Anton Hain.

MAIER, W. (1980): Nasal structures in Old and New World primates. In: Evolutionary Biology of the New World Monkeys and Continental Drift. Ed. by R. L. Ciochon and A. B. Chiarelli. New York, London: Plenum Press, pp. 219–241.

MOYNIHAN, M. (1970): Some behavior patterns of platyrrhine monkeys II. *Saguinus geoffroyi* and some other tamarins. Smithson. Contrib. Zool. **28**, 1–77.

OMEDES, A. (1981): Behavioural repertoire of adult silvery marmosets *Callithrix a. argentata* and *Callithrix a. melanura*. Misc. Zool. **7**, 193–211.

PERKINS, E. M. (1969a): The skin of primates. XL. The skin of the cottontop pinche *Saguinus* (= *Oedipomidas) oedipus*. Am. J. Phys. Anthropol. **30**, 13–28.

— (1969b): The skin of primates. XXIV. The Skin of Goeldi's marmoset *(Callimico goeldii)*. Am. J. Phys. Anthropol. **30**, 231–250.

— (1969c): The skin of primates. XLI. The skin of the silver marmoset – *Callithrix* (= *Mico) argentata*. Am. J. Phys. Anthropol. **30**, 361–388.

PRESLOCK, J. P.; HAMPTON, S. K.; HAMPTON, J. K., Jr. (1973): Cyclic variations of serum progestins and immunoreactive estrogens in marmosets. Endocrinol. **92**, 1096–1101.

SCHWARTZ, G. G.; ROSENBLUM, L. A. (1980): Novelty, arousal, and nasal marking in the squirrel monkey. Behav. Neural Biol. **28**, 116–122.

SPRANKEL, H. (1971): Zur vergleichenden Histologie von Hautdrüsenorganen im Lippenbereich bei *Tarsius bancanus borneanus* Horsefield 1821 und *Tarsius syrichta carbonarius* Linnaeus 1758. In: Proc. 3rd International Congress of Primatology, Zurich 1970, Vol. **1**. Ed. by H. Kummer. Basel: S. Karger. pp. 189–197.

STEVENSON, M. F.; POOLE, T. B. (1976): An ethogram of the common marmoset *(Callithrix jacchus jacchus)*: general behavioural repertoire. Anim. Behav. **24**, 428–451.

SUTCLIFFE, A. G.; POOLE, T. B. (1978): Scent marking and associated behaviour in captive common marmosets *(Callithrix jacchus jacchus)* with a description of the histology of scent glands. J. Zool., Lond. **185**, 41–56.

VOLAND, E. (1978): Darstellung und Klassifizierung individueller Verhaltensprofile von gefangengehaltenen Halbaffen (*Galago demidovii* Fischer, 1808) auf der Grundlage eines faktoranalytisch gewonnenen Systems von Verhaltenskategorien. Doctoral Diss. University of Göttingen.

ZELLER, U.; EPPLE, G.; KÜDERLING, I.; KUHN, H.-J. (1988): The anatomy of the circumgenital scent gland of *Saguinus fuscicollis* (Callitrichidae, Primates). J. Zool., Lond. **214**, 141–156.

ZELLER, U.; RICHTER, J.; EPPLE, G.; KUHN, H.-J. (in press): Die Circumgenitaldrüse von Krallenaffen der Gattung *Saguinus*. Verh. Anat. Ges.

Authors' addresses: Dr. ECKHARD W. HEYMANN and Dr. MICHAEL H. SCHWIBBE, Deutsches Primatenzentrum, Kellnerweg 4, D-3400 Göttingen; Dr. ULRICH ZELLER, Abt. Morphologie, Zentrum Anatomie der Universität Göttingen, Kreuzbergring 36, D-3400 Göttingen

Z. Säugetierkunde 54 (1989) 276–285

ISSN 0044-3468

Der Einfluß postnataler Geruchserfahrung auf das Verhalten der weißen Labormaus *(Mus musculus)*

Von HEIKE DIEKMANN und U. SCHMIDT

Zoologisches Institut, Poppelsdorfer Schloß, Universität Bonn

Eingang des Ms. 17. 2. 1988

Abstract

Influence of postnatal odor experience in laboratory mice (Mus musculus)

Investigated was the behavior of laboratory mice (strain NMRI) at different stages of development to specify, whether mice change their response to an artificial rearing odor.

From day of birth (day 0) to day 13 pp the dams of 48 siblings (experimental group) were impregnated with geraniol (10 % in paraffine) twice a day, while the dams of 41 youngs (control group) were not. During days 1 to 14 pp the behavior of the preweanlings was observed in three different two-choice-preference-tests. The control mice and the experimental group showed no differential behavior in response to the test odors "nest bedding" and cyclohexanone, which was unknown to both groups. Geraniol was avoided by the control mice, but was tolerated by the experimental ones. This effect is due to a physiological adaptation of the exposed mice to their artificial rearing odor.

Several times between day 20 pp and 60 pp the juvenile and adult mice were tested in a four-choice-preference-test (one position was odorized, three were not). Starting with day 20/30 the mice of both groups showed a constant behavior towards an odor, they had not become familiar with in the nest. In contrast, the response of the experimental mice to their rearing odor geraniol changed as follows: the 20 days old ♀♀ and ♂♂ (preweanlings) preferred geraniol, the 30 and 40 days old mice behaved indifferently, the exposed adult ♂♂ (60 days old) avoided their exposure odor. We found the behavior of the adult ♀♀ of both groups being dependent on the stage of sexual cycle. The control ♀♀ avoided geraniol in oestrus, the experimental ♀♀ in dioestrus and prooestrus.

Einleitung

Nagetiere setzen den Geruchssinn in vielen Situationen während ihres ganzen Lebens zur Kommunikation und Orientierung ein. Dabei kann die Geruchserfahrung während der ersten Lebenstage Einfluß auf das Verhalten der Tiere nehmen (CHEAL 1975; D'UDINE und ALLEVA 1983; ALBERTS 1982, 1986). So wird z. B. bei jungen Ratten das erste, olfaktorisch geleitete Suchen nach den Zitzen der Mutter durch die Geruchserfahrungen in utero oder während des Geburtsvorganges beeinflußt (TEICHER und BLASS 1976, 1977; PEDERSEN und BLASS 1982; STICKROD et al. 1982; PEDERSEN et al. 1983). Kürzere oder längere Duftstoff-Expositionen während der ersten Lebenstage können bei Ratten das für junge Nager charakteristische Nestsuchverhalten dahingehend verändern, daß sie den Expositionsduft gegenüber einem fremden Duft bevorzugen (CORNWELL-JONES 1979; CAZA und SPEAR 1984).

Wie in „cross-fostering"-Experimenten nachgewiesen werden konnte, wird selbst die Zuordnung zu „Artgenossen" durch olfaktorische Stimuli, die im Nest erfahren wurden, bestimmt: Im Sozialpräferenztest bevorzugten Mäuse die Individuen der „foster"-Species (Ratte, *Baiomys tailori*) gegenüber Artgenossen (HUDGENS et al. 1968; QUADAGNO und BANKS 1970). Die Aufzucht mit parfümierten Eltern oder Geschwistern lieferte Hinweise darauf, daß für die Sexualpartnerwahl ebenfalls Duftreize, die die Mäuse im Nest kennenlernten, von Bedeutung sein können (MAINARDI et al. 1965; OEDBERG 1976; D'UDINE und ALLEVA 1983).

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5405-0276 $ 02.50/0

Auch anatomische und physiologische Veränderungen in Abhängigkeit von den in der Jugend erfahrenen Düften ließen sich nachweisen. Langandauernde Duftexpositionen wirken sich z. B. auf die Größe und den physiologischen Zustand der Mitralzellen im primären Riechhirn aus (Döving und Pinching 1973; Laing et al. 1985; Panhuber 1985, 1986). Durch Summenpotential- und Einzelzellableitungen aus dem Bulbus olfactorius konnte gezeigt werden, daß bei adulten Mäusen, die in den ersten zwei Lebenswochen in Geranioldduft aufgezogen worden waren, die neuronalen Antworten auf den Expositionsduft wesentlich höher waren als bei nichtbedufteten Kontrolltieren (Eckert 1985; Reinken und Schmidt 1987).

In verhaltensphysiologischen Experimenten sollten nun Hinweise auf die bisher ungeklärte Frage erarbeitet werden, wie im Nest erfahrene Düfte von Labormäusen in unterschiedlichen Altersstadien bewertet werden.

Material und Methode

Versuchstiere

48 Labormäuse (Stamm NMRI; 24 ♀♀, 24 ♂♂) wurden während der ersten 14 Lebenstage (Tag 0 bis 13) dem aliphatischen Alkohol Geraniol ($C_{10}H_{17}OH$) exponiert, indem wir ihre Muttertiere zweimal täglich mit einer 10%igen Lösung dieses Duftstoffes am Bauch einstrichen. Da die Aufzuchtkäfige abgedeckt und mit gefilterter Luft (250 ml/min) durchströmt waren, konnten die Jungtiere neben dem Expositionsduft nur die natürlicherweise im Nest vorkommenden Gerüche (Muttertier, Geschwister, wenig duftendes Körnerfutter) wahrnehmen. Als Einstreu diente Fließpapier, das täglich erneuert wurde. Die Kontrollgruppe (21 ♀♀, 20 ♂♂) wuchs in einer entsprechenden Aufzuchtanlage auf, jedoch ohne Imprägnation der Muttertiere mit Geraniol.

Ab Tag 14 hielten wir die Würfe beider Gruppen im Tierraum des Instituts; die Käfige wurden nicht mehr abgedeckt, so daß die Mäuse dauernd geruchlichen Kontakt zu adulten Artgenossen hatten. Am 30. Tag wurden die Jungtiere von der Mutter entfernt und nach Geschlecht getrennt. Regelmäßiges Wiegen der Versuchsmäuse ermöglichte eine dauernde Kontrolle ihrer Entwicklung; außerdem wurde in allen Versuchen ihre lokomotorische Aktivität festgehalten. Alle zwei Tage reinigten wir die für die Aufzucht verwendeten Gegenstände gründlich mit heißem Wasser und einer duftfreien Seifenlösung (Extran™).

Die Geraniol-exponierten Mäuse unterschieden sich hinsichtlich der Gewichtsentwicklung und der lokomotorischen Aktivität nicht von der Kontrollgruppe. Lediglich der Zeitpunkt des Augenöffnens war um etwa einen Tag verzögert.

Versuchsanlage

Nestlinge (Tag 1–14)

In den ersten zwei Lebenswochen wurde das Verhalten der infantilen Mäuse täglich in verschiedenen Zweifachwahl-Anlagen beobachtet, in denen den Versuchsmäusen die Duftreize in unterschiedlicher Weise angeboten werden konnten.

Im Glasdüsentest strömte gefilterte (Aktivkohle) und angefeuchtete Luft durch zwei parallel geschaltete Waschflaschen, die mit Duftsubstanzen beschickt werden konnten. Die Testdüfte waren:
a. der Nestduft des jeweiligen Wurfes vom Versuchstag,
b. Geraniol und
c. das zyklische Keton Cyclohexanon ($C_6H_{10}O$);
die beiden synthetischen Substanzen als 10%ige Lösung in Paraffin. Die Luftströme wurden den Versuchstieren durch zwei einander gegenüber ausmündende Glasdüsen zugeführt (Durchströmungsmenge: je 80 ml/min); durch eine der Glasdüsen wurde ein beduftteter Luftstrom geleitet, durch die andere die duftlose Leerprobe. Der Abstand zwischen den Öffnungen der Röhren betrug von Tag 1 bis Tag 5 fünf cm, von Tag 6 bis Tag 14 sieben cm. Als zusätzlicher taktiler Reiz lag vor den Öffnungen je eine Watteflocke. Der Boden der Versuchsarena bestand aus einer Glasplatte, unter der ein Registrierbereich (Kreisdurchmesser: 14 cm) und ein Indifferenzstreifen (Breite: 1 cm) markiert waren. Die Jungtiere wurden in zufälliger Reihenfolge zu Beginn eines Versuchsdurchgangs auf den Indifferenzstreifen aufgesetzt und je 60s beobachtet. Dabei registrierten wir, wie lange sich die Nase der Maus in einer der beiden Registrierhälften befand. Wir testeten täglich jede Maus mit den drei Testdüften, wobei von Tag zu Tag die Testreihenfolge zwischen „Nestduft–Cyclohexanon–Geraniol“

und „Geraniol–Cyclohexanon–Nestduft" wechselte. Vor jedem Versuchsdurchgang wurden die Glasplatte und die Glasdüsen mit Isopropanol gereinigt und die Watteflocken erneuert.

Ab dem 7. Tag führten wir nach dem Glasdüsentest zwei weitere Tests alternierend durch:

Beim Papierschnitzeltest, am Tag 6, 8, 10 und 12, wählten die Mäuse zwischen zwei Häufchen Fließpapierschnitzeln, von denen eines duftlos und das andere in konzentriertem Geranioldampf imprägniert worden war (Methode: Schmidt et al. 1983). Der Abstand zwischen den Papierhäufchen entsprach der eineinhalbfachen Körperlänge der Versuchsmäuse. Auch hier betrug die Beobachtungszeit pro Tier 60s; es wurde die Dauer des direkten Kontakts mit einem Papierhäufchen aufgezeichnet.

Im Verdunstungsschalentest, am Tag 7, 9, 11 und 13, bewegten sich die Mäuse auf einem gelochten Boden, unter dem konzentriertes Geraniol verdampfte. Wir werteten aus, wie lange sich eine Maus direkt über der Geraniolquelle aufhielt.

Während der Tests wurden die Jungtiere von dem Muttertier getrennt auf einer Wärmeplatte (33 °C) gehalten. Um eine Beeinflussung der Reaktion durch gerichtete Reize aus der Umgebung möglichst gering zu halten, veränderten wir bei jedem Test von Tier zu Tier die Ausrichtung der Versuchsanlage im Raum, die Ausgangslage der Versuchstiere und die Position der Duftgabe, und die Experimentatorin hielt sich immer in der Symmetrieachse der Anlagen auf. Alle Gegenstände, die mit den Versuchstieren oder den Duftmolekülen in Kontakt kamen, wurden täglich oder von Wurf zu Wurf mit heißem Wasser und einer geruchlosen Seifenlösung gereinigt.

Juvenile und adulte Mäuse (20.–60. Lebenstag)

Am 20., 30., 40. und 60. Lebenstag wurden die Mäuse in einer Vierfachwahl-Anlage (Röhrentest) untersucht. Die Reizquellen waren hier vier Kunststoffröhren, unter denen Blockschälchen mit den Duftsubstanzen verborgen waren. Es war jeweils eine Reizquelle mit 10%igem Geraniol oder Cyclohexanon beschickt, die anderen drei enthielten als Leerproben Paraffin. Die Beobachtungszeit betrug je 5 min, und es wurde registriert, wie lange die Tiere Kontakt mit den Röhren hielten. Bei den adulten, 60 Tage alten ♀♀ wurde das Verhalten an 5 aufeinanderfolgenden Tagen beobachtet und die Zyklusphase durch Vaginalabstriche bestimmt (Allen 1922; Fabian 1964).

Auswertung

Da nicht von normal-verteilten Stichproben ausgegangen werden konnte, wurde für die statistischen Berechnungen der Mann-Whitney-U-Test verwendet. In allen Diagrammen (außer Abb. 3) sind die Mediane der Aufenthaltsdauer der Mäuse an der bedufteten Reizquelle und an der Leerprobe aufgetragen. In den hier vorgestellten Untersuchungen wurden in den nicht-parametrischen statistischen Tests für jeden Tag die Aufenthaltsdauer an der Duftquelle mit der an der Leerprobe verglichen. In den Abbildungen wurden die Balkenpaare markiert, deren Unterschied mit wenigstens 5%iger Ablehnungswahrscheinlichkeit sicherbar war (*: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$, –: $p > 0.05$).

Ergebnisse

Als Nestlinge bevorzugten sowohl die Kontrollen als auch die experimentellen Mäuse im Glasdüsentest ihren Nestduft zwischen Tag 6 (bzw. 5) und Tag 12 (bzw. 13) deutlich, d. h. sie hielten sich an der Nestduftdüse länger auf als an der Leerprobendüse (Abb. 1). Die Testreihenfolge hatte auf die Nestduft-Reaktion beider Gruppen keinen Einfluß; immer war die Nestbevorzugung gleich gut, unabhängig davon, ob Nestduft als erster oder dritter Duft getestet wurde (Abb. 2).

Auf Cyclohexanon reagierten die Mäuse beider Aufzuchtgruppen indifferent; auch dieses Verhalten war von der Testreihenfolge unabhängig.

Im Glasdüsentest lehnten die Kontrolltiere das Geraniol zwischen Tag 5 und 9 ab (Abb. 1). Die Geraniol-exponierten Mäuse verhielten sich in diesem Alter indifferent gegenüber ihrem Aufzuchtgeruch. Für die Geraniol-Reaktion der Kontrolltiere spielte die Testreihenfolge keine Rolle, d. h. sie lehnten diese Duftsubstanz unabhängig von der Testreihenfolge ab (Abb. 2). Die exponierten Mäuse dagegen verhielten sich indifferent gegenüber dem Geraniol, wenn es als erstes, und lehnten es ab, wenn es als letztes getestet wurde.

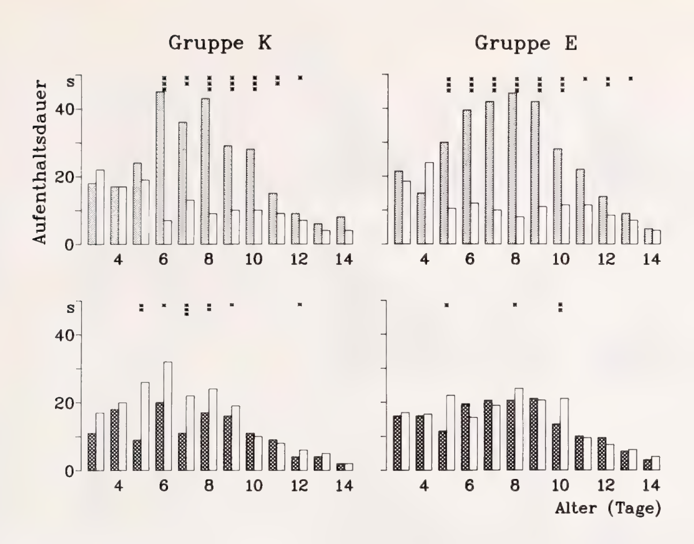
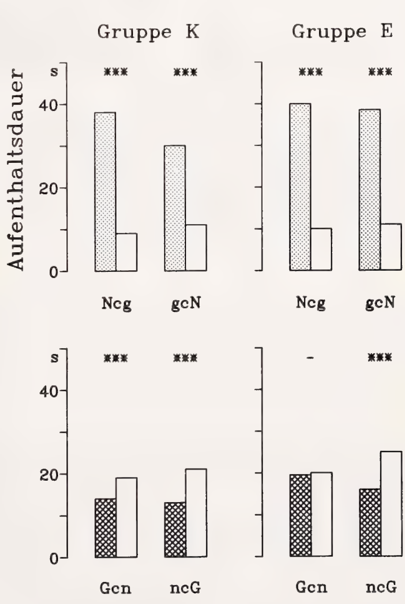


Abb. 1. Reaktionen der nestjungen Mäuse im Glasdüsentest (links: Kontrollgruppe, rechts: exponiert aufgezogene Mäuse). Es sind die Mediane der Aufenthaltsdauer an der Reizquelle mit Nestduft (punktierte Säulen), Geraniol (doppelt schraffiert) und an der Leerprobe (weiß) aufgetragen. Die Sterne kennzeichnen den Unterschied innerhalb eines Säulenpaares (***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$; Mann-Whitney-U-Test)



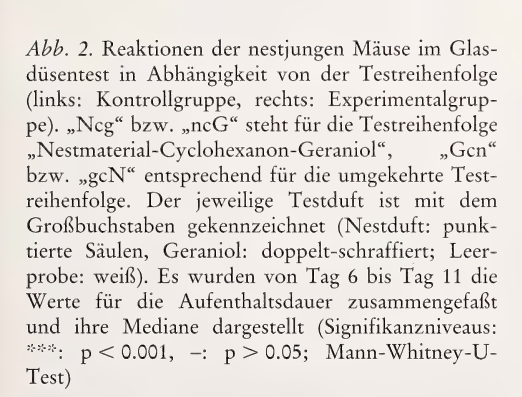


Abb. 2. Reaktionen der nestjungen Mäuse im Glasdüsentest in Abhängigkeit von der Testreihenfolge (links: Kontrollgruppe, rechts: Experimentalgruppe). „Ncg" bzw. „ncG" steht für die Testreihenfolge „Nestmaterial-Cyclohexanon-Geraniol", „Gcn" bzw. „gcN" entsprechend für die umgekehrte Testreihenfolge. Der jeweilige Testduft ist mit dem Großbuchstaben gekennzeichnet (Nestduft: punktierte Säulen, Geraniol: doppelt-schraffiert; Leerprobe: weiß). Es wurden von Tag 6 bis Tag 11 die Werte für die Aufenthaltsdauer zusammengefaßt und ihre Mediane dargestellt (Signifikanzniveaus: ***: $p < 0.001$, –: $p > 0.05$; Mann-Whitney-U-Test)

Im Papierschnitzeltest lehnten die Kontrolltiere das Geraniol an den Tagen 8, 10 und 12 ab (Tag 6: indifferentes Verhalten, $p = 0.0526$; Abb. 3). Die exponiert-aufgezogenen Mäuse verhielten sich wiederum eher indifferent gegenüber ihrem Aufzuchtgeruch (Tag 8: leichte Geraniol-Bevorzugung, $p = 0.0465$). Die experimentellen Mäuse hielten sich jedoch immer deutlich länger im Geraniol-Papier auf als die Kontrolltiere. Das Ergebnis des Verdunstungsschalentests entsprach im wesentlichen dem des Papierschnitzeltests.

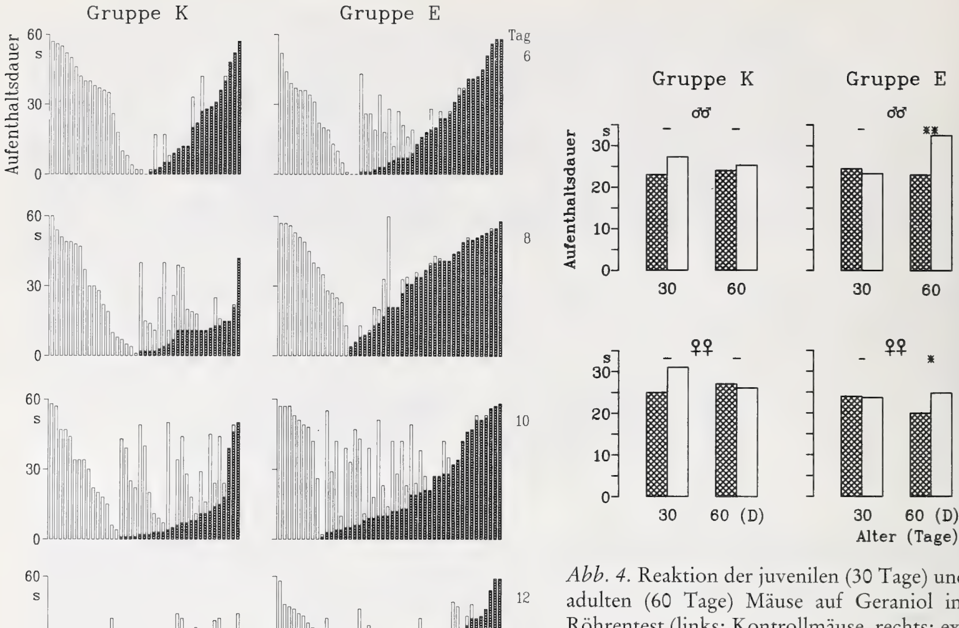


Abb. 3. Reaktion der Einzeltiere im Papierschnitzeltest im Alter von 6, 8, 10 und 12 Tagen. Die Aufenthaltsdauer im Geraniol-imprägnierten Papierhäufchen (doppelt-schraffierter Säulenteil) und im duftlosen Papierhäufchen (weiß) wurden aufeinander aufaddiert (links: Kontrollmäuse, n = 41; rechts: experimentelle Mäuse, n = 48)

Abb. 4. Reaktion der juvenilen (30 Tage) und adulten (60 Tage) Mäuse auf Geraniol im Röhrentest (links: Kontrollmäuse, rechts: exponiert-aufgezogene Mäuse; oben: ♂♂, unten: ♀♀). Zum Vergleich mit der Reaktion der ♂♂ wurde bei den adulten ♀♀ das Verhalten im Diöstrus (D) herangezogen. Abgebildet sind die Mediane der Aufenthaltsdauer an der mit Geraniol beschickten Röhre (doppelt-schraffierte Säulen) und an den nicht-bedufteten Röhren (weiß) (Signifikanzniveaus: ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$, –: $p > 0.05$; Mann-Whitney-U-Test)

Während bei den Nestlingen keine Unterschiede im Verhalten von ♀♀ und ♂♂ festgestellt werden konnten, mußte die Auswertung beim Röhrentest (ab Tag 20) nach Geschlecht getrennt erfolgen.

Geraniol erwies sich für die Kontroll-♂♂ als völlig neutraler Duft: in allen vier Altersstadien verhielten sich die Mäuse indifferent (Abb. 4). Bei den experimentellen ♂♂ dagegen wechselte die Bedeutung im Verlauf der Experimente: Mit 20 Tagen war eine leichte Bevorzugung zu verzeichnen, als Juvenile (Tag 30 und 40) beachteten sie das Geraniol nicht, als Adulte (Tag 60) lehnten sie ihren Expositionsduft ab. Beim Test mit Cyclohexanon verhielten sich die ♂♂ beider Aufzuchtgruppen im Alter von 20 Tagen indifferent, danach lehnten sie diese Substanz bis zum Alter von 60 Tagen deutlich ab (Abb. 5).

Die exponiert aufgezogenen und die Kontroll-♀♀ reagierten auf Geraniol im Alter zwischen 20 und 40 Tagen wie die entsprechenden, gleichaltrigen ♂♂. Cyclohexanon wurde von den Kontroll-♀♀ in diesem Zeitraum ebenfalls abgelehnt, die experimentellen ♀♀ verhielten sich indifferent.

Die Zykluslängen der ♀♀ beider Gruppen entsprachen der Norm. Während ca. 50 % der untersuchten Zeit befanden sich die Mäuse im Diöstrus, während je ca. 20 % im Östrus bzw. Metöstrus, und nur während 10 % im Proöstrus. Nur im Diöstrus gleicht die olfaktorische Sensitivität bei den ♀♀ der der ♂♂. In diesem Zyklusstadium entsprachen

auch die Reaktionen der ♀♀ auf die beiden Düfte denen der ♂♂, d.h. die Kontrollen beachteten die Geraniolröhre nicht (p = 0.121) und lehnten das Cyclohexanon ab (p = 0.007); die experimentelle Gruppe vermied ebenfalls Cyclohexanon (p = 0.00007), reagierte jedoch abweisend auf Geraniol (p = 0.018; Abb. 6). Durch den sehr geringen Stichprobenumfang im Proöstrus sind Aussagen für dieses Zyklusstadium nur bedingt möglich. Bei den Geraniol-♀♀ läßt sich auch hier eine Ablehnung des Aufzuchtduftes berechnen (p = 0.032), die Kontrollen lehnten Geraniol im Östrus ab (p = 0.012). Es konnte für keinen der beiden Düfte eine statistisch absicherbare Präferenz verzeichnet werden. Alle Meidereaktionen drückten sich ausschließlich in den Aufenthaltszeiten an den Röhren aus, die Kontakthäufigkeiten an den bedufteten und duftlosen Röhren waren ausgeglichen.

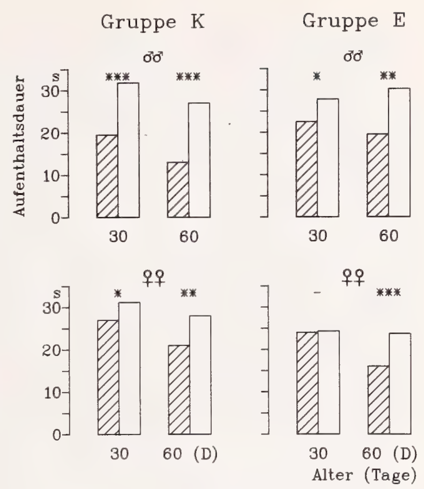


Abb. 5. Reaktion der juvenilen und adulten Mäuse auf Cyclohexanon (schraffiert) im Röhrentest (Erklärung s. Abb. 4.)

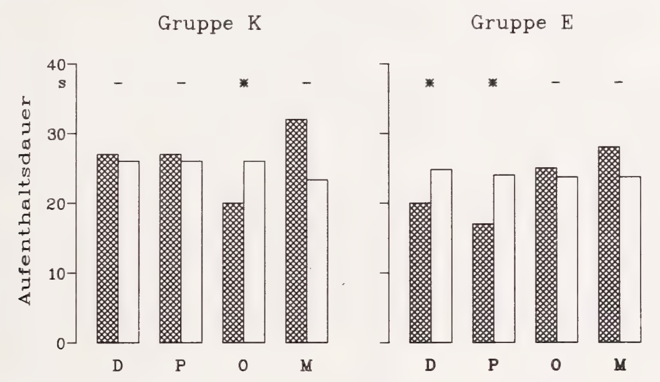


Abb. 6. Reaktion der adulten ♀♀ auf Geraniol im Röhrentest in Abhängigkeit vom Zyklusstadium. D = Diöstrus, P = Proöstrus, O = Östrus, M = Metöstrus (Erklärung s. Abb. 4.)

Diskussion

Unsere Untersuchungen waren in engem Bezug auf die elektrophysiologische Arbeit von Eckert (1985) projektiert. Es wurden daher der gleiche Mäusestamm (NMRI), der gleiche Expositionsgeruch (Geraniol) und der gleiche Expositionszeitraum (Tag 0 bis 13) verwendet. Der Duftstoff Geraniol erwies sich in vorhergehenden Untersuchungen als unschädlich für Mäuse und Experimentatoren (Eckert und Schmidt 1985); er ist daher für Langzeit-Untersuchungen gut geeignet. Um etwaige Unterschiede im Verhalten der exponiert aufgezogenen Mäuse und der Kontrollen besonders deutlich zutage treten zu lassen, wurde die Geruchsbeeinflussung gegenüber der früher angewandten verstärkt, indem das Geraniol den Jungtieren nicht nur in der Luft zugeführt, sondern auf den Bauch der Mutter aufgetragen wurde. Es zeigte sich, daß diese intensive Duftstoffexposition die physiologische Entwicklung der Mäuse nicht beeinträchtigte.

Das im Glasdüsentest bei Applikation von Nestduft provozierte Aufsuchen der Duftdüse entspricht dem für junge Nager charakteristischen Nestsuchverhalten (Ratten: Scer-

ZENIE und HSIAO 1977; Goldhamster: DEVOR und SCHNEIDER 1974; GREGORY und BISHOP 1975; CRANDALL und LEONARD 1979; Mäuse: SCHMIDT et al. 1983). Diese Reaktion wurde durch die frühe, langanhaltende Exposition mit Geraniol nicht verändert, und es war keinerlei Beeinträchtigung der olfaktorischen Diskriminierungsfähigkeit durch den sehr intensiven Expositionsduft feststellbar. Die von ECKERT (1985) unter Geraniol-Bedampfung aufgezogenen Mäuse zeigten ebenfalls eine unveränderte neuronale Reaktion auf ihren Nestgeruch.

Im Gegensatz zum Test mit Nestmaterial konnte beim Test mit Geraniol in allen drei Zweifachwahl-Anlagen ein unterschiedliches Verhalten bei den Mäusen der Kontroll- und der Experimentalgruppe im Alter zwischen 6 und 12 Tagen nachgewiesen werden. Während die Kontrollmäuse das Geraniol in diesem Zeitraum ablehnten, verhielten sich die exponierten Mäuse indifferent. Die Analyse der Daten in Abhängigkeit von der Testreihenfolge ergab jedoch, daß die Experimentalgruppe ihren Aufzuchtgeruch im Glasdüsentest nur dann tolerierte, wenn dieser als erster getestet wurde. War Geraniol der dritte Testduft, lehnten ihn auch die exponierten Mäuse ab. Dieser Effekt läßt sich als Auswirkung einer physiologischen Adaptation an den Expositionsgeruch interpretieren: Beim Testen des ersten Duftstoffes waren die Jungtiere erst wenige Minuten von dem nach Geraniol riechenden Muttertier getrennt; bis zum Test des dritten Duftes vergingen etwa 40–50 Minuten, so daß eine Deadaptation einsetzen konnte.

Im Papierschnitzeltest trat der Deadaptationseffekt nicht auf. Obwohl dieser Test immer nach dem Glasdüsentest durchgeführt wurde, tolerierten die experimentellen Mäuse ihren Aufzuchtgeruch. Verantwortlich für die unterschiedliche Auswirkung der Adaptation müssen die qualitativ und quantitativ unterschiedlichen Geraniolpräsentationen in den beiden Testsituationen sein. Im Glasdüsentest wurde den Jungtieren ein mit Geraniolmolekülen bedufteter Luftstrom angeboten, im Papierschnitzeltest diffundierte dagegen Geraniol von Nestmaterial-ähnlichem Fließpapier. Die jeweiligen Duftkonzentrationen sind nur schwer abzuschätzen; sie müssen aber in beiden Fällen überschwellig sein, da sie bei den Kontrolltieren eine deutliche Ablehnung hervorrufen.

Während das Verhalten der nestjungen Mäuse weitestgehend von naheliegenden, physiologischen Notwendigkeiten (Wärme, Nahrung) bestimmt wird, beeinflussen zahlreiche exogene und endogene Faktoren die Reaktionen der juvenilen und adulten Mäuse. Im Röhrentest zeigte es sich, daß die juvenilen ♂♂ (20, 30 und 40 Tage alt) ihr Verhalten gegenüber einem Duftstoff, den sie nicht in der Nestsituation kennengelernt haben, ab einem Alter von 20/30 Tagen bis zum Adultstadium (60 Tage) nicht mehr verändern. Das konnte zum einen beim Testduft Cyclohexanon festgestellt werden, der ja für die experimentelle und die Kontrollgruppe gleichermaßen unbekannt war: die ♂♂ beider Gruppen lehnten das Cyclohexanon ab Tag 30 durchgängig ab. Der gleiche Effekt trat auch beim Verhalten der Kontrollgruppe gegenüber dem Testduft Geraniol auf: die juvenilen und adulten Kontroll-♂♂ verhielten sich ab der 4. Lebenswoche indifferent. Die exponiert-aufgezogenen ♂♂ verändern dagegen mehrfach während ihrer Entwicklung zum Adulttier ihr Verhalten gegenüber ihrem Aufzuchtduft: Nur im Alter von ca. 3 Wochen bevorzugen sie das Geraniol. Zu diesem Zeitpunkt liegt die Geraniol-Exposition um 6 Tage zurück, die Entwöhnung ist aber noch nicht abgeschlossen. Es ist anzunehmen, daß sich die Mäuse in diesem Alter von der Geraniol-Adaptation erholt haben, daß sie aber das Geraniol im Nest mit positiven Stimuli (Mutter, Nahrung, Wärme) assoziiert haben. Das Ergebnis stimmt mit denen anderer Experimentatoren überein, die nach einer Geruchsexposition von infantilen Nagern eine Bevorzugung des Expositionsduftes im juvenilen Alter nachweisen konnten (Mäuse: GOLDBLATT 1978; Ratten: LEON et al. 1977; BRUNJES und ALBERTS 1979; CORNWELL-JONES 1979; GALEF und KANER 1980, GALEF 1982). Nach der Entwöhnung, im Alter von 30 und 40 Tagen, verhalten sich die experimentellen ♂♂ wie die Kontroll-♂♂ indifferent beim Test von Geraniol. Eine zeitliche Einschränkung der Präferenz eines Expositionsduftes beschrieben auch GALEF und KANER (1980) bei Ratten. Im Adultsta-

dium erfährt der im Nest erlebte Duft einen erneuten Bedeutungswandel. Während Autoren wie MAINARDI et al. (1965) und QUADAGNO und BANKS (1970) die Indifferenz von Mäuse-♂♂ gegenüber Düften, die sie postnatal erfahren haben, betonen, konnten wir eine deutliche Ablehnung des Expositionsduftstoffes durch die ♂♂ feststellen.

Das Verhalten der Mäuse-♀♀ ist in komplexer Weise vom Reproduktionsstatus abhängig. Von C. SCHMIDT (1979) wurde erstmals nachgewiesen, daß sich die Riechschärfe von Mäuse-♀♀ während des Sexualzyklusses in charakteristischer Weise verändert, was einen direkten Einfluß auf die Detektierbarkeit der Testsubstanzen haben kann. Unabhängig davon scheint sich aber auch das Interesse der ♀♀ an bestimmten Düften zyklusabhängig zu ändern. Mit dem Fortpflanzungsverhalten eng verbunden sind vor allem Proöstrus und Östrus, wobei man annehmen kann, daß während des Proöstrus, vielleicht auch schon im späten Diöstrus, eine Sexualpartnerwahl stattfindet, während im Östrus dann die Kopulationen erfolgen. Der Metöstrus ist für die Reproduktion weniger relevant, da er unter natürlichen Bedingungen kaum auftritt. Der Diöstrus gilt als asexuelles Zwischenstadium. Daher kann das Verhalten im Diöstrus als Maß für das Verhalten adulter ♀♀ herangezogen werden, das nicht unter direkter Beeinflussung durch das Fortpflanzungsverhalten steht. Berücksichtigt man nur den Diöstrus, stellt sich heraus, daß die adulten ♀♀ beider Gruppen das gleiche Verhalten gegenüber Geraniol und Cyclohexanon zeigen wie die ♂♂. Bei den exponierten ♀♀ verliert aber das Geraniol im Östrus und Metöstrus die aversive Komponente. Da sie das Geraniol jedoch nicht nur im Diöstrus, sondern auch im Proöstrus, also in der Zeit der Partnerwahl, ablehnen und im Hinblick darauf, daß auch die adulten ♂♂ der Experimentalgruppe den Expositionsduft meiden, könnte hier der Mechanismus einer Inzuchtbarriere zutage treten.

In verschiedenen Versuchsansätzen wurde erarbeitet (MAINARDI et al. 1965; D'UDINE und ALLEVA 1983), daß die Selektion der Sexualpartner durch Mäuse-♀♀ von den olfaktorischen Reizen, die sie im Nest kennenlernten, beeinflußt werden kann. Dabei wirkt es sich für das ♂ begünstigend aus, wenn es der gleichen Subspecies wie der Vater des ♀, aber einer anderen Linie angehört („Vatereffekt", MAINARDI 1963a, 1963b). Die Annahme, daß die von uns beobachteten adulten Mäuse ihren Aufzuchtgeruch deshalb ablehnten, weil sie ihn mit der Erwartung eines nah verwandten Artgenossen verbanden, führt zu dem Schluß, daß in diesem Experiment der künstliche Aufzuchtgeruch Geraniol im Nest als ein olfaktorisches Charakteristikum für die Familienzugehörigkeit aufgenommen worden ist.

Danksagung

Unser Dank gilt der Deutschen Forschungsgemeinschaft für die Finanzierung dieser Untersuchung (Schm 322/7).

Zusammenfassung

Bei weißen Labormäusen (Stamm NMRI) wurde in verschiedenen Entwicklungsstadien untersucht, ob sich nach intensiver Duft-Exposition während der ersten 14 Lebenstage das Verhalten gegenüber dem künstlichen Aufzuchtgeruch verändert.

Die Muttertiere von 48 Jungtieren wurden in deren ersten zwei Lebenswochen zweimal täglich mit einer 10%igen Geraniollösung eingestrichen. Die Mütter der Kontrollgruppe (41 Jungtiere) blieben unbehandelt. Das Verhalten der nestjungen Mäuse wurde von Tag 1 bis Tag 14 täglich in drei verschiedenen Zweifach-Präferenzwahlanlagen untersucht. Die exponierten Mäuse und die Kontrollen zeigten keinen Unterschied im Verhalten auf ihren Nestgeruch und auf den für beide Gruppen unbekannten Duftstoff Cyclohexanon. Die Kontrolltiere lehnten das Geraniol ab, während die exponierten Mäuse eine größere Toleranz zeigten. Dieser Effekt ist auf eine Adaptation der experimentellen Mäuse an ihren Aufzuchtgeruch zurückzuführen.

Die juvenilen und adulten Mäuse wurden zwischen dem 20. und 60. Tag mehrfach in einer Vierfach-Wahlsituation getestet (eine Position wurde mit Duft beschickt, die drei übrigen Positionen blieben unbeduftet). Es zeigte sich, daß die Reaktion der Mäuse auf einen Duftstoff, den sie nicht im

Nest kennengelernt hatten, ab einem Alter von 20/30 Tagen gleich bleibt. Die exponiert-aufgezogenen Mäuse dagegen veränderten mehrfach ihr Verhalten gegenüber ihrem Aufzuchtgeruch: Nur vor der Entwöhnung, im Alter von ca. 3 Wochen, bevorzugten die ♀♀ und ♂♂ das Geraniol, am 30. und 40. Lebenstag verhielten sie sich indifferent. Die exponiert-aufgezogenen adulten ♂♂ (Tag 60) lehnten den Geranioldurft deutlich ab. Bei den adulten ♀♀ beider Gruppen war die Reaktion auf Geraniol abhängig vom Sexualzyklus. Die Kontrollen lehnten diesen Duft im Östrus, die Geranioltiere dagegen im Di- und Proöstrus ab.

Literatur

Alberts, J. R. (1982): Ontogeny of olfaction: issues and perspectives from contemporary research. In: Olfaction and Endocrine Regulation. Ed. by W. Breipohl. London: IRL Press. 161–172.

— (1986): Postnatal development of olfactory-guided behavior in rodents. In: Ontogeny of Olfaction. Ed. by W. Breipohl. Berlin: Springer Verlag. 227–235.

Allen, E. (1922): The oestrus cycle in the mouse. Am. J. Anat. **30**, 297–348.

Brunjes, P. C.; Alberts, J. R. (1979): Olfactory stimulation induces filial preferences for huddling in rat pups. J. Comp. Physiol. Psychol. **93**, 548–555.

Caza, P. A.; Spear, N. E. (1984): Short-term exposure to an odor increases its subsequent preference in preweanling rats: A descriptive profile of the phenomenon. Dev. Psychobiol. **17**, 407–422.

Cheal, M. (1975): Social Olfaction: A review of the ontogeny of olfactory influences on vertebrate behavior. Behav. Biol. **15**, 1–25.

Cornwell-Jones, C. A. (1979): Olfactory sensitive periods in albino rats and golden hamsters. J. Comp. Physiol. Psychol. **93**, 668–676.

Crandall, J. E.; Leonard, C. M. (1979): Developmental changes in thermal and olfactory influences on golden hamster pups. Behav. Neural Biol. **26**, 354–363.

Devor, M.; Schneider, G. E. (1974): Attraction to home-cage odor in hamster pups: Specifity and changes with age. Behav. Biol. **10**, 211–221.

Döving, K. B.; Pinching, A. J. (1973): Selective degeneration of neurones on the olfactory bulb following prolonged odour exposure. Brain Res. **52**, 115–129.

Eckert, M. (1985): Zum Einfluß frühjugendlicher Geruchsbelastungen auf die neuronalen Reizantworten des Bulbus olfactorius bei Labormäusen. Dissertation, Bonn.

Fabian, G. (1964): Methylblau als Übersichtsfärbung von Vaginalabstrichen. Z. Wissensch. Mikr. **66**, 210–212.

Galef, B. G. (1982): Acquisition and waning of exposure-induced attraction to a nonnatural odor in rat pups. Dev. Psychobiol. **15**, 479–490.

Galef, B. G.; Kaner, H. C. (1980): Establishment and maintenance of preference for natural and artificial olfactory stimuli in juvenile rats. J. Comp. Physiol. Psychol. **94**, 588–595.

Goldblatt, A. (1978): Effect of early olfactory experience on a tilt table odor preference. Behav. Biol. **22**, 269–273.

Gregory, E. H.; Bishop, A. (1975): Development of olfactory-guided behavior in the golden hamster. Physiol. Behav. **15**, 373–376.

Hudgens, G. A.; Denenberg, V. H.; Zarrow, M. X. (1968): Mice reared with rats: Effects of preweaning and postweaning social interactions upon adult behaviour. Behav. **30**, 259–274.

Laing, D. G.; Panhuber, H.; Pittman, E. A.; Willcox, M. E.; Eagleson, G. K. (1985): Prolonged exposure to an odor or deodorized air alters the size of mitral cells in the olfactory bulb. Brain Res. **336**, 81–87.

Leon, M.; Galef, B. G.; Behse, J. H. (1977): Establishment of pheromonal bonds and diet choice in young rats by odor pre-exposure. Physiol. Behav. **18**, 387–391.

Mainardi, D. (1963a): Speziazione nel topo. Fattori etologici determinanti barriere riproduttive tra *Mus musculus domesticus* e *M. m. bactrianus*. Istituto Lombardo (Rend. Sc.) B **97**, 135–142.

— (1963b): Eliminazione della barriera etologica all'isolamento riproduttivo tra *Mus musculus domesticus* e *M. m. bactrianus* mediante azione sull'apprendimento infantile. Istituto Lombardo (Rend. Sc.) B **97**, 291–299.

Mainardi, D.; Marsan, M.; Pasquali, A. (1965): Causation of sexual preferences in the house mouse. The behaviour of mice reared by parents whose odour was artificially altered. Atti. Soc. ital. Sci. nat. **104**, 325–338.

Oedberg, F. (1976): Failure to demonstrate imprinting on an artificial odour in two strains of mice. Biology of Behaviour **1**, 309–327.

Panhuber, H. (1985): Prolonged exposure to odours leads to topographic changes in the olfactory bulb, and altered behaviour. Neurosci. Lett. Suppl. **19**, 10.

— (1986): The effect of long duration postnatal odour exposure on the development of the rat olfactory bulb. In: Ontogeny of Olfaction. Ed. by W. Breipohl, Berlin: Springer Verlag. 127–141.

Pedersen, P. E.; Blass, E. M. (1982): Prenatal and postnatal determinants of the 1st suckling episode in albino rats. Dev. Psychobiol. **15**, 349–355.

Pedersen, P. E.; Stewart, W. B.; Greer, C. A.; Shepherd, G. M. (1983): Evidence for olfactory function in utero. SCI **221**, 478–480.

Quadagno, D. M.; Banks, E. M. (1970): The effect of reciprocal cross fostering on the behaviour of two species of rodents, *Mus musculus* and *Baiomys taylori ater*. Animal. Behav. **18**, 379–390.

Reinken, U.; Schmidt, U. (1987): Dependence of single unit activity in the olfactory bulb on early odor experience in the laboratory mouse. Naturwiss. **74**, 555–556.

Scerzenie, V.; Hsiao, S. (1977): Development of locomotion toward home nesting material in neonatal rats. Dev. Psychobiol. **10**, 315–321.

Schmidt, C. (1979): Elektrophysiologische und verhaltensphysiologische Untersuchungen zum Riechvermögen der weißen Labormaus *(Mus musculus)*. Diss., Univ. Bonn.

Schmidt, U.; Eckert, M.; Schäfer, H. J. (1983): Untersuchungen zur ontogenetischen Entwicklung des Geruchssinnes bei der Hausmaus *(Mus musculus)*. Z. Säugetierkunde **48**, 355–362.

Stickrod, G.; Kimble, D. P.; Smotherman, W. P. (1982): In utero taste/odor aversion conditioning in the rat. Physiol. Behav. **28**, 5–7.

Teicher, M. H.; Blass, E. M. (1977): First suckling response of the newborn albino rat: The roles of olfaction and amniotic fluid. SCI **198**, 635–636.

d'Udine, B.; Alleva, E. (1983): Early experience and sexual preferences in rodents. In: Mate Choice. Ed. by P. Bateson. Cambridge: Cambridge University Press. 311–327.

Anschrift der Verfasser: Dipl. Biol. Heike Diekmann und Prof. Dr. Uwe Schmidt, Zoologisches Institut, Universität Bonn, Poppelsdorfer Schloß, D-5300 Bonn

Z. Säugetierkunde 54 (1989) 286–295

ISSN 0044-3468

Démographie et dispersion d'une population sauvage insulaire de *Mus musculus domesticus:* comparaison avec une population continentale

Par MARIA NAVAJAS Y NAVARRO, J. CASSAING et H. CROSET

Institut des Sciences de l'Evolution, Laboratoire d'Eco-éthologie, Université des Sciences et Techniques du Languedoc, Montpellier, France

Reception du Ms. 1. 2. 1988

Abstract

Demography and dispersal of one feral insular population of Mus musculus domesticus: comparison with one mainland population

The demography and the dispersal of feral mice *Mus musculus domesticus* on the Island of Corsica were studied and compared to those of a mainland population in Southern France. Both populations displayed similar trends in density, with annual peaks in autumn or winter and lows in summer. However, the average density of mice per hectare on the island (4 to 22) was higher than on the mainland (0,5 to 7) and the mainland population showed greater fluctuations of the number of individuals. Local movements on the study area were significantly lower in the island where the mice were more sedentary, except in autumn. Several factors concerning the arrangement of the insular community and habitat (niche expansion, competition and predation pressure) were analysed to explain the features found in the island population. Data suggest that these environmental traits may be necessary but not sufficient for explaining the differences, and an intrinsically regulated population mechanism and social factors are suggested to account for the demographic and dispersal patterns in the Corsica population.

Introduction

Les communautés insulaires présentent généralement un ensemble de caractéristiques qui les distinguent de leurs homologues continentales: l'appauvrissement de la faune; l'élargissement de la gamme de biotopes utilisables par une espèce en l'absence de certains compétiteurs; la diminution de la pression de prédation en raison du moindre nombre de prédateurs. Chez les Rongeurs, le changement de niche en situation insulaire a souvent été attribué au relâchement des pressions de compétition et à la réduction de la prédation. En liaison avec ce changement de niche, on observe alors une réduction de la capacité de dispersion (CROWELL 1973; SULLIVAN 1977; TAMARIN 1977a), une augmentation des densités (Sullivan 1977; TAMARIN 1977a; GLIWICZ 1980; CROWELL 1983; ADLER et al. 1986; GRANJON et CHEYLAN 1988), mais parfois aussi une diminution de cette densité (DELANY 1970; ADLER et TAMARIN 1984), une réduction de l'agressivité (HALPIN et SULLIVAN 1978) ainsi que la modification d'autres traits démographiques ou sociaux (GLIWICZ 1980) et plus généralement un ensemble de modifications qui amène les populations vers une stratégie démographique de type «K» (BERRY et JAKOBSON 1975; TAMARIN 1977b, 1978).

Ainsi, le relâchement de la compétition interspécifique et l'isolement vis-à-vis des populations continentales peuvent faire apparaître, dans les îles, les conditions nécessaires à une différenciation géographique de l'espèce, voire à une évolution rapide vers la spéciation. La comparaison de la biologie des populations continentales et insulaires d'une même espèce permet de répondre aux questions suivantes:
– Quels sont les traits biologiques modifiées entre les deux types du situation?

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5405-0286 $ 02.50/0

- Si des modifications sont mises en évidence, la situation d'isolement a-t-elle entraîné un «syndrome d'insularité» compararable à celui observé pour d'autres espèces (et donc généralisable)?
- Quel est le rôle des caractéristiques environnementales (autres que l'isolement lui-même) et celui des réaménagements de la communauté?
- Quelles sont les mécanismes (sélectifs, effects stochastiques) mis en jeu dans cette différenciation?

La souris domestique, *Mus musculus domesticus* Rutty, que nous utilisons comme modèle pour tenter de répondre à ces questions, est souvent la seule espèce du genre *Mus* présente dans les îles de la Méditerranée occidentale (Alcover 1979, 1983; Orsini 1982; Cheylan 1984) tandis que sur le continent, dans le Sud de la France et en Espagne, elle vit en sympatrie, voire en syntopie avec *Mus spretus* Lataste (Britton-Davidian et Thaler 1978). L'interaction entre les deux espèces de souris a été documentée sur le plan écologique (Orsini et al. 1982; Cassaing et Croset 1985), éco-physiologique (Sicard et al. 1985; Navajas y Navarro 1987), génétique (Navajas y Navarro et Britton-Davidian 1989) et comportemental (Cassaing 1984).

Libois (1984) a montré que l'extension de l'amplitude d'habitat de *Mus musculus domesticus* en Corse ne faisait aucun doute: pour deux stations écologiquement équivalentes (i.e. mêmes zonations climatiques, altitudinales, phytosociologiques, mêmes grands types d'habitats) l'Indice d'Amplitude d'Habitat de Piélou (1969) est égal à 2,49 dans les Pyrénées Orientales et 3,54 en Corse.

Il nous a donc paru intéressant de rechercher si l'élargissement de niche de *M. m. domesticus* et l'appauvrissement de la faune en Corse s'accompagnait d'une augmentation des densités de cette espèce (phénomène de compensation de densités) et d'une tendance à la sédentarité. Les résultats seront discutés en référence à une population continentale précédemment étudiée (Orsini et al. 1982; Cassaing et Croset 1985); nous nous proposons donc dans ce travail de mettre en évidence des différences éventuelles dans la démographie et la dynamique de l'occupation de l'espace entre une population insulaire et une population continentale de *M. m. domesticus,* et de rechercher le rôle de l'insularité à travers son double aspect «isolement» et «particularité du milieu».

Nous tenterons ainsi de répondre aux aspects écologiques présentés dans les questions posées ci-dessus. L'analyse des mécanismes mis en jeu dans la différentiation des populations insulaires fait l'objet de travaux en cours dont les résultats seront publiées par ailleurs.

Matériel et méthodes

Situations géographiques et écologiques

1. Station insulaire

Elle est située sur la côte Nord-Ouest de la Corse, dans la baie d'Elbo (réserve naturelle de Scandola). Un quadrat de 3,76 hectares a été échantillonné; il comprend cinq faciès de végetation:

- Milieu A (il represénte 35 % de la surface totale échantillonnée):
  Des friches à *Inula viscosa, Ferula communis, Euphorbia helioscopia.* La présence de nombreuses Papillonacées et surtout Graminées y déterminent de Juin à Octobre une abondance de petites graines dont les souris se nourissent.
- Milieu B (15 % du quadrat): Une zone dégradée à *Cistus monspeliensis* et *Polygonum scoparium* sur sol rocheux avec touffe de *Pistacia lentiscus.*
- Milieu C (environ 10 % du quadrat): Un *Oleo-lentiscetum* sur rocher avec *Erica arborea, C. monspeliensis, P. lentiscus, Phillyrea latifolia, Ph. angustifolia, Olea europaea.*
- Milieu D (entre 5 et 10 % du quadrat): Un maquis élevé à *Arbutus unedo, E. arborea, Ph. latifolia, Viburnum tinus.*
- Milieu E (30 % du quadrat): Une zone à *P. lentiscus* dense au bord des ruisseaux avec *Ph. latifolia, V. tinus.*

La maille de piègeage utilisée est de 20 m, conformément aux observations réalisées sur le continent par Duplantier et al. (1984a): dans une zone très ouverte comme en Petite Camargue, ces auteurs ont

montré que les déplacements importants des micromammifères justifiaient l'emploi d'une maille de piégeage de 30 m. A Elbo, le milieu est relativement fermé et semblable aux garrigues languedociennes dans lesquelles une maille de 20 m est préférable. Seule l'utilisation d'une maille adéquate et d'une grille de dimensions suffisantes permet à la fois une estimation correcte des effectifs et des déplacements individuels: c'est pourquoi il nous a paru plus important, dès lors qu'il s'agit de comparer des caractéristiques spatiales de populations naturelles, d'utiliser une méthodologie appropriée à la situation, cas par cas. A chaque point de capture, deux pièges grillagés «Firobind» appâtés avec un mélange de farine et de sardine ont été disposés le soir et relevés le lendemain matin.

Quatre espèces de micromammifères ont été capturées: *Rattus rattus, Apodemus sylvaticus, M. m. domesticus* et *Crocidura suaveolens.*

2. *Station continentale.*Les données de la population continentale ont été obtenues à partir d'un quadrat situé en Petite Camargue. Cette station est un complexe dunaire entre mer et étang, avec des bas-fonds inondables, des zones sableuses colmatées et des dunes.

En plus des 4 espèces de micromammifères présentes à Elbo, dans cette zone se trouvent aussi *Eliomys quercinus, Rattus norvegicus, Microtus agrestis* et Crocidura russula.

Le choix des dimensions de ce quadrat (18 ha) ainsi que la maille de piégeage (30 m) ont fait l'objet d'une étude approfondie (Duplantier et al. 1984a; 1984b); les grands déplacements observés le justifient amplement. La description de cette station et les résultats obtenus ont été publiés par ailleurs (Orsini et al. 1982; Cassaing et Croset 1985).

Estimation des paramètres démographiques

Les animaux capturés sont pesés, marqués par amputation des phalanges, puis relachés à l'endroit de leur capture. L'effort de piégeage est poursuivi jusqu'à ce que 80 % des animaux soient marqués. Ce résultat est obtenu après 4 nuits de piégeage en moyenne. Une recapture est effectuée 3 jours plus tard, ce qui permet une estimation des effectifs. Six sessions d'échantillonnage se sont succédées tous les 3–4 mois.

L'estimation des effectifs a été réalisée par l'application de l'indice de Lincoln. Les distributions des densités estimées au cours des saisons dans les deux populations (île, continent) ont été comparées par un test de signe (Siegel 1956).

Nous avons évalué le renouvellement de la population par le taux de disparition (T) des individus marqués, comme pour la population continentale de référence (Cassaing et Croset 1985), d'après la formule suivante: $T = M - m/M \times 100$, où M est le nombre d'individus marqués à la session s et m le nombre d'individus marquès à la session $s + 1$. Ce résultat est rapporté au nombre de mois passés entre les deux sessions. Pour le calcul des divers paramètres démographiques, les animaux de poids supérieur à 13 g ont été considérés comme adultes.

Déplacements et sédentarité

Nous avons utilisé la Distance Maximale de Recapture (DMR), de Spitz (1969), comme mesure des déplacements. Cette mesure décrit la partie du domaine vital utilisée pendant une session de piégeage: nous utiliserons donc la DMR comme un estimateur du domaine vital à l'instant t. Pour ce faire, nous avons mesuré la distance linéaire maximale qui sépare deux points de capture, puis nous avons calculé une moyenne par sexe et par saison.

Le Déplacement Saisonnier de l'Activité (DSA) a été calculé d'après la méthode décrite par Cassaing et Croset (1985), en mesurant le déplacement linéaire du centre d'activité théorique (assimilé au centre géométrique des points de capture); il permet d'estimer le déplacement global de la population, ou d'une catégorie d'individus, entre deux saisons d'échantillonnage. L'indice de Sédentarité (LS) entre deux saisons est alors déterminé en rapportant la distance obtenue précédemment à la moyenne des DMR pour deux saisons successives. Un Indice de 1 signifie que la population est restée globalement sedentaire; des valeurs comprises entre 1 et 1.5 peuvent être interprétées comme un glissement d'aire d'activité d'une partie ou de toute la population. Un IS supérieur à 1.5 signifie qu'il y a eu migration ou dispersion (Cassaing et Croset 1985).

Les distributions des valeurs des DMR et DSA s'étant avérées non gaussiennes, elles ont été analysées par un test non paramétrique (U de Mann-Whitney).

Résultats

Population d'Elbo (Corse)

Démographie: Au cours de l'année, on observe deux périodes de renouvellement de la population: la première se situe entre janvier et avril (Tab. 1, Fig. 1). Entre avril et juillet la population est en repos reproducteur et ne présente quasiment aucun renouvellement: il existe une chute de la densité, qui peut être attribuée à la mortalité mais aussi, pour une part, à la mobilité des individus (IS = 1,5, Tab. 2). Les individus qui se répartissent en hiver pour ⅓ dans le milieu A, ⅓ également dans le milieu E, le reste se trouvant surtout dans le milieu B, vont se concentrer pour 60 à 70 % dans les frîches à Graminées (milieu A) en été et au début de l'automne. La population se caractérise en juillet par un sex-ratio nettement déséquilibré (1,9, Tab. 1), avec un excès de mâles.

La deuxième période de renouvellement, entre juillet et octobre, est la plus importante. Le pourcentage d'adultes qui était de 95 % en juillet se réduit progressivement pour arriver à 61 % en octobre; on peut donc penser que ce sont les individus nés sur le quadrat qui contribuent à ce renouvellement de la population. C'est à l'automne que la mobilité des animaux est la plus grande (IS = 2,8, Tab. 2). Cela traduit une réorganisation spatiale de la population qui pourrait être liée à la disparition des anciens résidents.

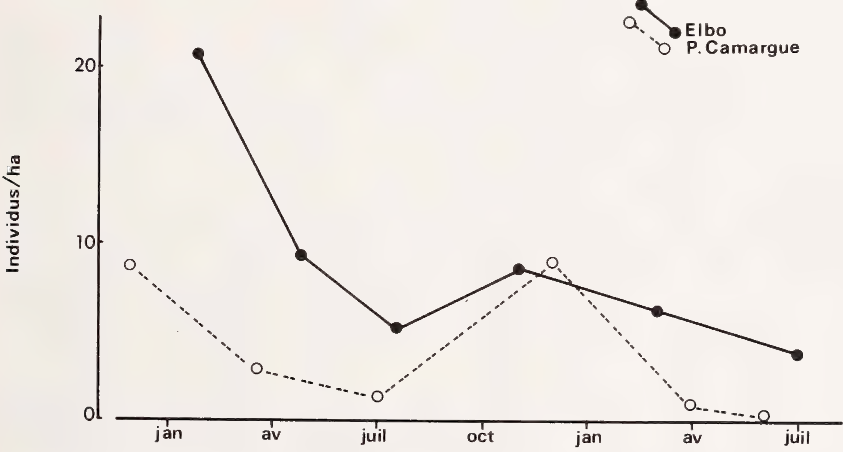


Fig. 1. Variations de densité de *Mus musculus domesticus* à Elbo, Corse et sur le continent en Petite Camargue. Les effectifs sont estimés par l'indice de Lincoln

Tableau 1. **Paramètres démographiques de *Mus musculus domesticus*** à Elbo (Corse), **au cours de six sessions de piégeage**

	janvier 1984	avril 1984	juillet 1984	octobre 1984	mars 1985	juillet 1985
Effectif capturé	56	37	20	31	15	13
Effectif estimé (indice de Lincoln)	73	37	20	33	17	13
Proportion d'adultes dans la population	41 %	51 %	95 %	61 %	60 %	85 %
Sex ratio	1	1,25	1,9	1,6	2	1,6
Taux de renouvellement (par mois)	12 %	2 %	19 %	9 %	19 %	

Tableau 2. **Déplacements instantanés (Distance Maximale de Recapture = DMR), Déplacement Saisonnier de l'Activité (DSA) et Indice de Sédentarité (IS) de *Mus musculus domesticus* à Elbo (Corse) au cours de six sessions de piégeage**

Les données sont exprimées en mètres: moyenne, minimum-maximum (effectif)

	janvier 1984	avril 1984	juillet 1984	octobre 1984	mars 1985	juillet 1985	moyenne ± écart type
DMR							
mâles	25,4 0–100 (12)	24,3 0–45 (17)	41,3 0–100 (10)	28,1 0–63 (16)	28,2 20–45 (5)	24,2 0–45 (5)	28,6 ± 5,9
femelles	14,2 0– 82 (10)	26,0 0–45 (12)	26,5 0– 82 (6)	14,4 0–81 (7)	14,0 0–28 (2)	18,3 0–45 (4)	18,9 ± 5,4
total	20,3	25,0	35,8	27,2	24,1	21,6	25,7 ± 5,1
DSA							
mâles	48,5 (5)	33,8 (8)	20,3 (2)	75,3 (6)	–		
femelles	7,0 (1)	59,8 (6)	41,4 (2)	82,5 (2)	141 (1)		
total	41,6 0–152	44,9 0–180	30,5 0– 55	77,1 5–181	141		
IS							
mâles	1,9	1,0	0,6	2,7	–		
femelles	0,6	2,3	2,0	5,8	–		
total	1,8	1,5	1,0	2,8	–		

Déplacements et sédentarité: Les déplacements de la souris à Elbo ne diffèrent guère au cours des saisons et la Distance Maximale de Recapture (DMR) est de 26 m en moyenne (Tab. 2). Cette moyenne, assez faible, concerne les adultes comme les subadultes, et contient en toutes saisons une certaine proportion de DMR nulle: 54 % en janvier, 21 % en avril, 25 % en juillet, 30 % en octobre 1984, 14 % en mars et 33 % en juillet 1985.

Les résultats de mesure de la DMR montrent qu'à Elbo les domaines explorés par la souris sont plus importants, en moyenne, chez les mâles (DMR = 29 m) que chez les femelles (DMR = 19 m). En raison de la forte variabilité individuelle, la différence n'est pas significative; néanmoins, ce phénomène est observé régulièrement, sauf en avril 1984. En juillet les mâles montrent des domaines plus étendus qu'en toute autre saison (DMR = 41 m).

Le suivi dans le temps des individus peut être estimé par la mesure du Déplacement Saisonnier de l'Activité (DSA). Les valeurs de DSA, qui vont de 7 à 82 m, comparées à celles de la DMR au cours d'une même session (26 m en moyenne), montrent qu'il n'y a pas eu, sauf certains cas, dispersion. Si l'on regarde les valeurs individuelles de DSA, on observe qu'en effet, une dispersion s'est produite pour une proportion très faible d'individus: le centre d'activité de janvier et celui d'avril 1984, pour le mâle numéro 56, sont distants de 125 m; le DSA moyen pour le reste des individus n'est alors qui de 19 m et l'indice de sédentarité devient 0,86 (au lieu de 1,8). La même situation est observée entre avril et juillet 1985, avec un individu qui déplace son centre d'activité de 180 m: l'indice de sédentarité devient 1,1 (au lieu de 1,5).

On peut donc dire que la population d'Elbo est globalement sédentaire de janvier à octobre, avec toutefois quelques mouvements au printemps: l'indice de sédentarité des ⅔ des individus, mâles et femelles, est inférieur à 1,5. La période suivante, soit l'automne, montre une mobilité plus générale avec une femelle dont le centre d'activité s'est decalé de 120 m (le domaine vital étant à ce moment de 14 m) et 6 mâles dont le centre d'activité s'est decalé de 75 m en moyenne: 2/8 individus seulement restent sédentaires.

Comparaison avec la population continentale

Les fluctuations d'abondance au cours de l'année ont des patrons similaires chez les populations insulaire (Elbo) et continentale (Petite Camargue) de *M. m. domesticus* (Fig. 1). Toutefois, les variations absolues restent plus fortes sur le continent, où les effectifs passent de moins de 0,5 à 7 individus/ha (ils sont multipliés par un facteur 14); en revanche à Elbo ils passent de 4 à 22 individus/ha (soit un facteur 5). Les deux populations ont leur densité maximale en automne/hiver et minimale au printemps/été. Mais dans l'île la densité est plus élevée en toutes saisons ($p = 0{,}031$); elle est en moyenne deux fois plus éllevée que sur le continent. La période de reproduction est plus courte sur le continent puisqu'elle commence en été et se termine au début de l'hiver, tandis que sur l'île elle se prolonge jusqu'au début du printemps.

Les déplacements sont multipliés par un facteur quatre sur le continent, avec une DMR moyenne de 112 m chez les mâles et 85 m chez les femelles, contre 28 m et 19 m respectivement, en Corse (Fig. 2). Les déplacements très réduits de la souris à Elbo contrastent avec ceux de l'espèce en Petite Camargue, où la DMR avoisine ou dépasse 100 m en toutes saisons.

Les faibles valeurs de DSA de la population insulaire contrastent également avec celles de Petite Camargue, surtout pour la période printemps/été ($p < 0{,}05$, Fig. 3). La souris à Elbo est assez sédentaire: une faible proportion d'individus présente un décalage important de l'activité d'une saison à l'autre, sauf en automne, et les déplacements instantanés sont très restreints, particulièrement pour les femelles. En revanche, des mouvements de dispersion affectent la moitié de l'effectif en Petite Camargue au printemps, aussi bien pour les màles que pour les femelles et les domaines instantanés sont étendus à toutes périodes pour les deux sexes également.

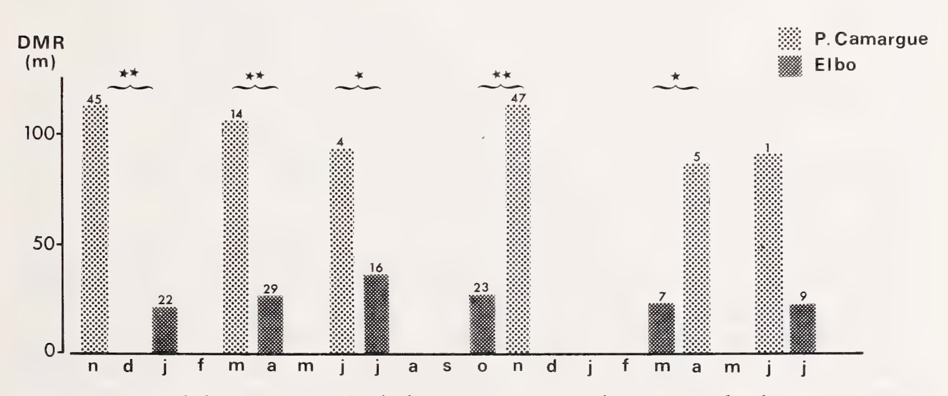


Fig. 2. Variations de la Distance Maximale de Recapture (DMR) de *Mus musculus domesticus* au cours de l'année à Elbo, Corse et sur le continent en Petite Camargue. Pour chaque saison de piégeage, les deux populations sont comparées par un test de Mann-Whitney (**: $p < 0{,}001$; *: $p < 0{,}05$). Les effectifs sont indiqués pour chaque mois

Discussion

A Elbo *M. m. domesticus* presente une densité plus élevée que son homologue continental de Petite Camargue. Une explication des fortes densités souvent observées dans les îles est apportée par le modèle de MacArthur et Wilson (1963) qui montre une corrélation négative entre la richesse des communautés et la densité des populations. Ce phénomène, qui a été nommé «compensation de densités» (MacArthur et al. 1972) implique que dans une île, l'espèce a la possibilité de réaliser une niche plus large, ce qui se traduit par

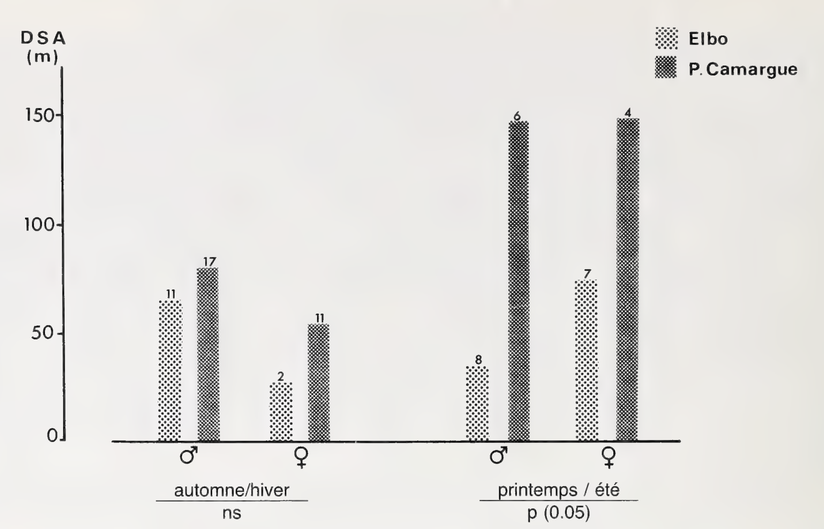


Fig. 3. Variations du Déplacement Saisonnier de l'Activité (DSA) de *Mus musculus domesticus* à Elbo, Corse et sur le continent en Petite Camargue. Les deux populations sont comparées par un test de Mann-Whitney (ns = non significatif). Les effectifs sont indiqués pour chaque mesure

l'augmentation des densités, par rapport aux régions continentales qui entretiennent une plus grande richesse spécifique.

Dans le Sud de la France, où cette espèce se trouve en sympatrie avec *M. spretus,* l'étude de la répartition écologique (Orsini et al. 1982) montre qu'elle occupe préférentiellement des habitats plus humides que *M. spretus.* Bien que par ses caractéristiques physiologiques *M. m. domesticus* paraisse moins apte à occuper les biotopes secs (Sicard et al. 1985), nous l'avons trouvée dans le Sud de la Corse dans des Garrigues sèches sur calcaire, comparables aux milieux occupés par *M. spretus* sur le continent. L'utilisation de ces biotopes sur les îles a été également montrée en Sardaigne (Orsini 1982) et aux îles Baléares (Alcover 1983). Ces observations, comme celles de Libois (1984), montrent un élargissement de la gamme des biotopes occupés par la souris en Corse.

Toutefois, la corrélation entre composition de la communauté, l'élargissement de niche et la densité n'est pas prouvée. Ainsi, des cas de diminution de densité ont été signalés chez les rongeurs (Berry 1968; Adler et Tamarin 1984; Granjon et Cheylan 1988), dans des situations où la faune est appauvrie.

La prédation, invoquée pour expliquer l'augmentation de densités des populations insulaires notament par Crowell (1983), est qualitativement reduite en Corse (absence de *Mustela putorius, Genetta genetta, Martes foina, Strix aluco, Malpolon monspessulanus, Elaphe scalaris, E. longissima*). La stratégie de chasse ou la densité de prédateurs insulaires, comme *Tyto alba* (Libois 1984), peuvent toutefois compenser ces absences.

En conditions insulaires, il y a géneralement une réduction des mouvements de disperson (Sullivan 1977; Gliwicz 1980), ce qui peut être une cause d'augmentation des densités. Cette réduction est alors imputable au confinement. Une telle situation existe à Elbo: en effet, bien que la Corse soit une île de grande superficie, la zone occupée par la souris à Elbo est un vallon encaissé de quelques hectares, limité par la mer et un maquis dense et xérique où la souris est absente. Cette situation assez générale en Corse où la souris colonise surtout les zones littorales (Granjon et Cheylan 1988). Ceci doit conduire à une forte fragmentation des populations sur la côte ouest, montagneuse, et la souris doit donc éprouver des difficultés de dispersion, ce qui pourrait jouer un rôle dans la densité atteinte par les populations. Cependant en zone ouverte (Sud et Est de la Corse) les

populations insulaires de souris atteignent des densités équivalentes à celles observées à Elbo (données non publiées). La fragmentation et donc l'isolement relatif des populations ne paraît pas une cause suffisante à elle seule pour expliquer l'augmentation de densité.

Des facteurs intrinsèques ont également un rôle à jouer dans les modifications des paramètres (densité et dispersion) en situation insulaire. Ainsi, l'effort de reproduction est souvent réduit, par suite de la modification d'un ou plusieurs traits biologiques (cf revue de Gliwicz 1980): période d'élevage réduite, maturation tardive des femelles, nombre limité de femelles participant à la reproduction, taille réduite des portées. Cette réduction de l'effort de reproduction serait une réponse à la situation de confinement, et concernerait donc les petites îles. En effet, on observe en Corse une réduction de la taille des portées (Navajas y Navarro et Cheylan 1986), ce qui pourrait s'expliquer par la fragmentation du peuplement de souris; par contre, l'allongement de la période de reproduction, qui agit en sens inverse par rapport à la densité, serait imputable à la modification globale des conditions écologiques, notament une période plus prolonguée des ressources alimentaires disponibles.

A Elbo, les résultats montrent une réduction du domaine exploité par rapport à la situation continentale. En Petite Camargue le milieu est globalement ouvert et entièrement colonisé par la souris. Par contre, à Elbo les milieux ne sont pas tous occupés de la même façon, les milieux à bas recouvrement végétal (milieux A et B) étant préférentiellement colonisés par la souris. Le rat, *Rattus rattus,* peut contribuer à la confiner dans ces milieux: il occupe des micro-habitats disjoints de ceux de la souris (milieux C et D) d'où il peut l'exclure (Granjon et Cheylan 1988). Mais les mouvements opérés par la souris au printemps, qui l'amène à se déplacer vers les frîches où elle s'installe en été (cf indice de sédentarité) semblent liées à la disponibilité en ressources. C'est en effet en été que les graminées qui s'y trouvent en abondance fournissent les graines qui sont la base de son alimentation. Un partage de l'espace au sein de ces micro-habitats se ferait alors vraisemblablement par l'occupation de domaines de dimensions petites mais suffisantes pour fournir une diète adéquate.

On peut maintenant tenter d'interpreter l'ensemble des modifications que présente cette population corse de *M. m. domesticus* par rapport à son homologue continental. La Corse est en elle-même de dimensions trop importantes pour constituer une «île» pour cette espèce. Mais sa situation latitudinale, au Sud du littoral français, sa nature rocheuse et siliciceuse, et enfin les caractéristiques climatiques dues à l'insularité créent des conditions écologiques différentes de celles du littoral de Petite Camargue. Si on y ajoute l'absence du principal compétiteur continental, l'autre espèce de souris *Mus spretus,* ces conditions se sont avérées propices, pour *M. m. domesticus,* à un élargissement de niche dont on a vu toutefois qu'il n'était pas généralisable à l'échelle du micro-habitat. La fragmentation géographique des zones favorables à cette espèce surajoute alors à ces nouvelles conditions écologiques un phénomène d'«archipel» à son peuplement, structuré en petites «îles» avec un isolement relatif entre elles. Certains traits biologiques généralement signalés en situation insulaire apparaissent dès lors: réduction du domaine vital, faible dispersion, amortissement des fluctations annuelles d'effectifs, réduction de la taille des portées. Ces modifications s'accordent avec une stratégie démographique de type «K», dont on sait qu'elle est prédominante dans les îles. Plus généralement ces aménagements s'inscrivent dans le type de «stratégie de survie en milieu insulaire» décrite par Blondel (1986).

Notre analyse fait clairement apparaître qu'on ne peut relier de façon simple la modification d'un paramètre, comme l'augmentation de densité, avec un unique facteur externe (réduction de la compétition, relâchement de la prédation, répartition des ressources) ou interne à la population (restriction du domaine vital, effort de reproduction). C'est l'action simultanée de ces différents facteurs qui opèrent à la fois au niveau de l'individu et au niveau de la population pour amener celle-ci à une régulation adéquate vis-à-vis des conditions environnementales. Ces mécanismes de régulation sont spécifiques

(i.e. propre à *M. m. domesticus*) et s'exprimeraient par une stratégie d'occupation de l'espace et des comportement sociaux différents de ceux rencontrés sur le continent; c'est ce que les premières données relatives aux interactions interindividuelles dont nous disposons laissent apparaître (Cassaing et Navajas y Navarro, en préparation). Ces recherches permettront de mieux dégager les pressions sélectives impliquées dans l'évolution de ces populations de souris.

Remerciements

Le travail de terrain en Corse a été rendu possible par le soutien logistique du Parc Régional de Corse: nous sommes très reconnaissants aux personnes de cet Organisme pour l'aide matérielle qu'ils nous ont apporté. Nous tenons également à remercier ici à J. C. Auffray, G. Cheylan, J. P. Clara, R. Fons, L. Granjon et O. Pouliquen, qui ont participé au travail de terrain. Le financement des recherches a été assuré pour partie par le Centre National de la Recherche Scientifique dans le cadre du contrat d-ATP «Biologie de populations», pour partie par le Parc Régional de Corse.

Résumé

La démographie et la dispersion d'une population sauvage de souris *Mus musculus domesticus,* ont été étudiées sur l'île de Corse et comparées à celles d'une population continentale du Sud de la France. La densité suit la même tendance chez les deux populations: elle est maximale en automne ou en hiver et minimale l'été. Or, la population continentale a des fluctuations d'effectifs plus importantes. La densité moyenne est plus élevée sur l'île (4 à 22 souris/ha) que sur le continent (0,5 à 7). Les déplacements sont significativement reduits sur l'île, où la souris est plus sédentaire, sauf en automne. Dans cette étude les auteurs évaluent le rôle de divers facteurs relatifs au réaménagement des communautés (élargissement de la niche, pression de prédation et compétition), pour expliquer les caractéristiques de la population insulaire. Les données suggèrent que des changements des conditions environnementales n'ont pas nécessairement une action directe sur les mécanismes régissant la démographie et la dispersion de la population corse et ils sont plutôt liés à des facteurs sociaux et à des mécanismes de régulation intrinsèques à la population.

Zusammenfassung

Populationsdynamik und Aktionsräume freilebender Hausmäuse (Mus musculus domesticus) auf einer Insel: Vergleich mit einer Festlandpopulation

Die Demographie und die Größe und Veränderung der Aktionsräume freilebender Hausmäuse *(Mus musculus domesticus)* wurden in einer Population auf Korsika (Frankreich) untersucht und mit denen einer Festlandpopulation aus Südfrankreich verglichen. Die Dichte ist auf der Insel (4 bis 23 Individuen pro ha) größer als auf dem Festland (0,5 bis 7 pro ha). Im Jahreslauf ändern sich die Häufigkeiten in beiden Populationen in ähnlicher Weise. Die höchsten Dichten werden im Herbst und Winter, die geringsten im Sommer erreicht. Die Individuenzahl schwankt auf dem Festland stärker als auf der Insel. Mit Ausnahme des Herbstes sind die Mäuse auf der Insel ortstreuer als auf dem Festland und haben kleinere Aktionsräume. Nischenerweiterung, verminderte Konkurrenz und geringerer Feinddruck auf der Insel werden als mögliche Ursachen der Unterschiede zwischen den Populationen von Insel und Festland diskutiert.

Références

Adler, G. H.; Tamarin, R. H. (1984): Demography and reproduction in island and mainland white-footed mice *(Peromyscus leucopus)* in southeastern Massachusetts. Can. J. Zool. **62**, 58–64.

Adler, G. H.; Wilson, M. L.; Derose, M. J. (1986): Influence of island area and isolation on population characteristics of *Peromyscus leucopus.* J. Mammalogy **67**, 406–409.

Alcover, J. A. (1979): Els Mamifers de les Balears. Palma de Mallorca: Moll.

— (1983): Contribucio al coneixement dels mamifers de les Balears i Pitiüses: Carnivora, Rodentia. Thèse de Doctorat, Univ. Palma de Mallorca.

Berry, R. J. (1968): The ecology of an island population of the house mouse. J. Anim. Ecol. **37**, 445–470.

Berry, R. J.; Jakobson, M. E. (1975): Ecological genetics of an island population of the house mouse *(Mus musculus).* J. Zool. Lond. **175**, 523–540.

Blondel, J. (1986): Biogéographie évolutive. Paris: Masson.

Britton-Davidian, J.; Thaler, L. (1978): Evidence for the presence of two sympatric species of

mice (Genus *Mus* L.) in Southern France based on biochemical genetics. Biochem. Genet. **16**, 213–225.
CASSAING, J. (1984): Interactions intra- et interspécifiques chez les souris sauvages du Midi de la France, *Mus musculus domesticus* et *Mus spretus:* conséquences sur la compétition entre les deux espèces. Biol. Behav. **4**, 281–293.
CASSAING, J.; CROSET, H. (1985): Organisation spatiale, compétition et dynamique des populations sauvages de souris (*Mus spretus* Lataste et *Mus musculus domesticus,* Rutty) du Midi de la France. Z. Säugetierkunde **50**, 271–284.
CHEYLAN, G. (1984): Les Mamifères des îles de Provence et de la Méditerranée occidentale: un exemple de peuplement insulaire non équilibré? Rev. Ecol. (Terre Vie) **39**, 37–54.
CROWELL, K. L. (1973): Experimental zoogeography: introductions of mice to small islands. Am. Nat. **107**, 535–558.
CROWELL, K. L. (1983): Islands – Insights or artifacts? Population dynamics and habitat utilization in rodents. Oikos **41**, 442–454.
DELANY, M. J. (1970): Variation and ecology of island population of the long-tailed field mouse (*Apodemus sylvaticus,* L.). Symp. Zool. Soc. Lond. **26**, 283–295.
DUPLANTIER, J. M.; ORSINI, P.; THOHARI, M.; CASSAING, J.; CROSET, H. (1984a): Echantillonnage des populations de Muridés: influence du protocole de piégeage sur l'estimation des paramètres démographiques. Mammalia **48**, 129–141.
DUPLANTIER, J. M.; CASSAING, J.; ORSINI, P.; CROSET, H. (1984b): Utilisation des poudres fluorescentes pour l'étude du déplacement des petits Rongeurs dans la nature. Mammalia **48**, 25–30.
GLIWICZ, J. (1980): Island populations of rodents: their organisation and functioning. Biol. Rev. **55**, 109–138.
GRANJON, L.; CHEYLAN, G. (1988): Mécanismes de coexistence dans une guilde de muridés insulaires (*Rattus rattus* L., *Apodemus sylvaticus* L. et *Mus musculus domesticus* Rutty, en Corse): consequences évolutives. Z. Säugetierkunde **53**, 301–316.
HALPIN, Z. T.; SULLIVAN, T. P. (1978): Social interaction in island and mainland populations of the deer mouse, *Peromyscus maniculatus.* J. Mammalogy **59**, 395–401.
LIBOIS, R. M. (1984): Le régime alimentaire de la chouette effraie. Cahiers d'Ethologie Appliquée **4**, 1–202.
MACARTHUR, R. H.; DIAMOND, J. M.; KARR, J. R. (1972): Density compensation in island faunas. Ecology **53**, 330–342.
MACARTHUR, R. H. WILSON, E. O. (1963): An equilibrium theory of insular zoogeography. Evolution **17**, 373–387.
NAVAJAS Y NAVARRO, M. (1988): Réponse à la séchresse des populations naturelles de *Mus musculus domesticus:* différenciation adaptative ou acclimatation? In: Time scale and Water stress. Prc. 5th Int. Conf. on Mediterranean Ecosystems. Ed. by F. di Castri, Ch. Floret, S. Rambal. J. Roy. Paris: IUBS, 649–654.
NAVAJAS Y NAVARRO, M.; BRITTON-DAVIDIAN, J. (1989): Genetic structure of insular Mediterranean populations of the house mouse. Boil. J. Linn. Soc. (in press).
NAVAJAS Y NAVARRO, M.; CHEYLAN, G. (1986): Evolution de populations insulaires de *Mus musculus domesticus* et *Rattus rattus.* Coll. Nat. CNRS «Biologie des Populations». Univ. Lyon I, 442–446.
ORSINI, P. (1982): Facteurs régissant la répartition des souris en Europe: intérêt du modèle souris pour une approche des processus évolutifs. Thèse de Doctorat, Univ. Montpellier.
ORSINI, P.; CASSAING, J.; DUPLANTIER, J. M.; CROSET, H. (1982): Premieres données sur l'écologie des populations naturelles de souris *Mus spretus* et *Mus musculus domesticus* dans le Midi de la France. Rev. Ecol. (Terre Vie) **36**, 321–335.
PIELOU, E. C. (1969): An introduction to mathematical Ecology. New York: Wiley-InterScience.
SICARD, B.; NAVAJAS Y NAVARRO, M.; JACQUART, T.; LACHIVER, F.; CROSET, H. (1985): Métabolisme hydrique de populations de *Mus musculus domesticus,* RUTTY 1972, et *Mus spretus,* LATASTE 1883, soumises à divers régimes alimentaires. C. R. Acad. Sc. Paris **300**, III. 699–704.
SIEGEL, S. (1956): Non-parametric statistics for the behavioral sciences. New York: McGraw-Hill.
SPITZ, F. (1969): L'échantillonnage des petits mammifères. In: Problème d'Ecologie. L'échantillonnage des peuplements d'animaux en milieux terrestres. Paris: Masson.
SULLIVAN, T. (1977): Demography and dispersal in island and mainland populations of the deer mouse, *Peromyscus maniculatus.* Ecology **58**, 964–978.
TAMARIN, R. H. (1977a): Dispersal in island and mainland voles. Ecology **58**, 1004–1054.
— (1977b): Reproduction in the island beach vole, *Microtus breweri,* and the mainland meadow vole, *Microtus pennsylvanicus,* in Southeastern Massachusetts. J. Mammalogy **58**, 536–548.
— (1978): Dispersal, population regulation and k-selection in field mice. Am. Nat. **112**, 545–555.

Adresse des auteurs: MARIA NAVAJAS Y NAVARRO, JACQUES CASSAING et HENRI CROSET, Laboratoire d'Eco-Ethologie, Institut des Sciences de l'Evolution, Unité Associée au CNRS n° 327., Université des Sciences et Techniques du Languedoc, Place Eugène Bataillon, F-34060 Montpellier, cedex, France

Z. Säugetierkunde 54 (1989) 296–303

ISSN 0044-3468

On the occurrence of abnormal deciduous incisors during prenatal life in African "hystricomorphous" rodents

By W. P. Luckett, F. Schrenk and W. Maier

Department of Anatomy, University of Puerto Rico, San Juan, USA, and Institut für Biologie III, Universität Tübingen

Receipt of Ms. 8. 3. 1988

Abstract

Examined early stages of dental development in four families and five genera of African "hystricomorphous" rodents. Small, abnormal, anterior deciduous incisors (dI1) were detected in both jaws, anterior to the large, normal dI2, in early developmental stages of all species examined: *Bathyergus janetta, Georychus capensis, Ctenodactylus gundi, Pedetes caffer,* and *Anomalurops beecrofti.* These small, abnormal teeth develop an irregular dentinal knot, but lack ameloblasts and enamel; a similar morphogenetic pattern occurs in the anterior deciduous incisors of sciurids and probably represents the ancestral condition in rodents. The functional significance of these abnormal teeth during ontogeny remains to be determined.

Introduction

Following the initial descriptions of abnormal or vestigial incisors in fetal and perinatal sciurids (Freund 1892; Adloff 1898), murids (Woodward 1894), and castorids (Heinick 1908), it remained unclear whether these rudimentary teeth, which develop anterior to the larger gliriform incisors, are restricted to a few groups of rodents, or whether they have a broader distribution within the order. Moreover, the occurrence of these abnormal teeth appears to be variable within muroid and caviomorph rodents, as judged by published reports of their presence or absence. The rudimentary incisors have been studied most extensively in sciurids (Adloff 1898; Luckett 1985), where they appear to be a consistent feature of the prenatal dentition. A limiting factor in evaluating the distribution and possible functional significance of abnormal incisors in Rodentia is the relative lack of developmental studies of the dentition for most families of the order (see Luckett 1985).

Morphogenetic analysis indicates that the small, abnormal incisors of rodents are homologous with the first deciduous incisors (dI1) of the primitive eutherian dentition, and that the large gliriform incisors of the fetus and adult are dI2 (Luckett 1985). The ontogenetic and phylogenetic significance of rudimentary deciduous incisors in rodents remains to be elucidated, but a greater knowledge of their distribution in rodent families should provide additional insight into their biological role. To date, there appear to have been no developmental studies of the dentition for any of the African "hystricomorphous" or hystricognathous rodents. We use the term "hystricomorphous" in a structural rather than taxonomic context, especially in light of the uncertainties surrounding the phylogenetic relationships of the hystricomorphous but sciurognathous families Anomaluridae, Pedetidae and Ctenodactylidae (Wood 1985).

Studies are currently in progress on morphogenesis of the cranium in the hystricognathous family Bathyergidae (Maier and Schrenk 1987; Schrenk in press) and in the "hystricomorphous" families Anomaluridae, Pedetidae and Ctenodactylidae (Schrenk, in press). These investigations have also provided the opportunity to examine aspects of dental development in these same families. The present report will be limited to an analysis

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5405-0296 $ 02.50/0

of the incisive region in these taxa; a more detailed description of the entire dentition will be presented elsewhere (LUCKETT, in prep.).

Material and methods

Most of the fetuses examined during the present study were borrowed from the embryology collection of the Hubrecht Laboratory, Utrecht, the Netherlands, and from the Van der Horst Collection, Department of Zoology, University of the Witwatersrand, Johannesburg, South Africa (see Table 1). Fetal heads were doubly embedded in paraffin and celloidin, sectioned serially at 10–14μ, and stained with Azan. Serial sections of both jaws were examined histologically, in order to identify all developing tooth germs, and to homologize them by their relationships with each other and with adjacent skeletal elements and other landmarks of the fetal head.

Results

The stages of eutherian and rodent dental morphogenesis were described and illustrated in a previous publication (LUCKETT 1985) and will not be repeated here. The Table presents a summary of the most significant features of deciduous incisor development for each of the specimens examined during the present study.

Table 1. **Developmental aspects of deciduous incisors in the upper jaws of African rodents**

Species	Fetal length	dI^1	dI^2
Bathyergus janetta VDH Coll. Ba 1	13 mm CR	Moderate sized, abnormal, late bell, early dentin	Large, middle bell stage
Bathyergus janetta VDH Coll. Ba 2	21 mm CR	Moderate sized, abnormal dentinal cap	Very large, late bell, possible odontoblasts
Georychus capensis Hub. Lab. RO 436	30 mm CR	Small, abnormal dentinal knot	Huge tooth; thick dentin & enamel
Bathyergus janetta VDH Coll. Ba 3	48 mm CR	No trace	Huge tooth; thick dentin & enamel
Ctenodactylus gundi Hub. Lab. 208a	15.5 mm CR	Tiny, abnormal, thin dentinal cap	Large, early cap stage
Ctenodactylus gundi Hub. Lab. 213	22 mm CR	Tiny, abnormal, dentinal knot, partly fragmented	Large, middle bell stage
Ctenodactylus gundi Hub. Lab. 224a	32 mm CR	Tiny, abnormal, dentinal knot, partly resorbed	Large, late bell, moderately developed dentin
Ctenodactylus gundi Hub. Lab. 233	41 mm CR	Tiny, irregular dentinal knot, partly resorbed	Large; thick dentin, moderately developed enamel
Pedetes caffer Hub. Lab. RO 184	24 mm CR	Small, abnormal, late bell, thin dentinal arc	Moderately large, late bud-early cap stage
Anomalurops beecrofti P. Charles-Dominique Coll.	44 mm CR	Tiny, abnormal, dentinal cap, partly resorbed	Large tooth; thick dentin, moderately developed enamel

Family Bathyergidae

In the earliest stage of *Bathyergus* examined, a fetus of 13 mm crown-rump length (= CR), the large dI2 in both jaws are in the middle bell stage, with early differentiation of the stellate reticulum (Fig. 1). These teeth lie within the jaw stroma and are connected to the

oral epithelium by a short, slender dental lamina. The dental lamina disappears immediately distal to this tooth germ, so that there is no suggestion of dI3 in either jaw. Lying anterior (mesial) to the large dI2 is a smaller, moderate-sized, late bell dI1 in both jaws (Fig. 2). This tooth is more differentiated than dI2, in that it exhibits a distinct layer of

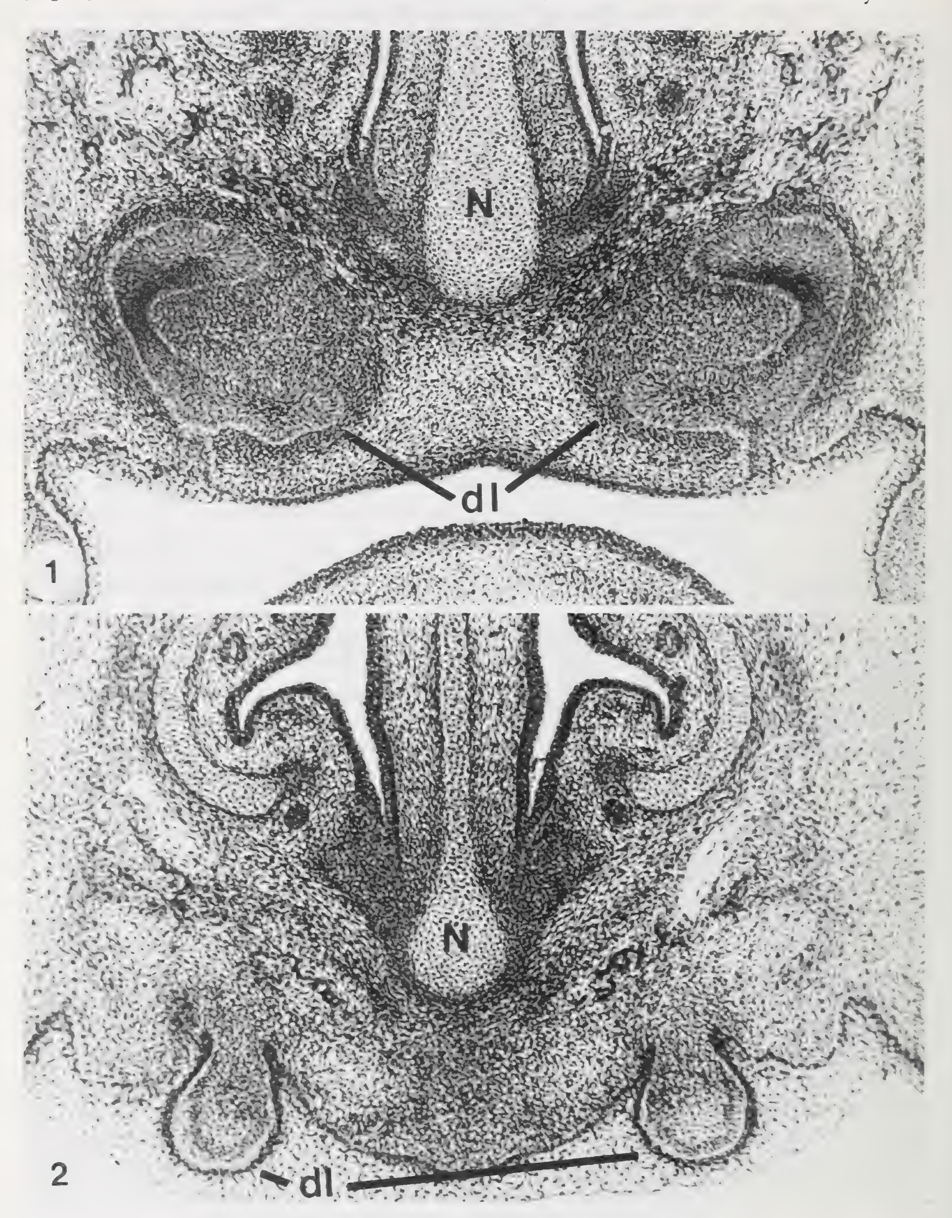


Fig. 1. Bathyergus janetta 13 mm CR fetus. Transverse section through upper jaw, showing the large, middle bell dI2 (dI), projecting into the jaw stroma, and overlain by the nasal septum (N). (×250). – *Fig. 2. Bathyergus janetta* 13 mm CR fetus. Transverse section through upper jaw, showing the small, abnormal bell stage dI1 (dI), projecting into the oral epithelium. Note the distinct, epithelioid layer of odontoblasts at the apex of the dental papilla. N = nasal septum. (×250)

odontoblasts and a thin layer of dentin or predentin. This anterior incisor is clearly abnormal, as indicated by its lack of stellate reticulum, and by the fact that it bulges into the overlying oral epithelium (Fig. 2). Consequently, the tooth germ retains a broad connection to the oral epithelium, so that a distinct dental lamina connection is not evident.

In a later fetus of 21 mm CR, the small to moderate-sized dI1 in both jaws consist of a densely cellular dental papilla overlain by a moderately developed dentinal cap, although a distinct layer of odontoblasts is lacking (Fig. 3). As in the previous stage, the abnormal tooth projects into the oral epithelium. There is no development of stellate reticulum, ameloblasts or enamel, and the outer and inner enamel epithelia are collapsed against each other, without differentiation. The more distal, greatly enlarged dI2 are in the late bell stage, with normal development of the stellate reticulum and an elongate dental lamina connection to the oral epithelium. Dentin has not yet formed on this tooth in the upper jaw, but a thin layer of dentin is developed on the lower dI2.

In a more mature 30 mm CR fetus of *Georychus capensis,* dI1 is represented only by a tiny, elongate, abnormal dentinal knot that projects into the oral epithelium of each jaw, and is connected to the underlying stroma by a slender connective tissue strand. This rudimentary tooth is closely followed by the enormous dI2, which possess thick dentin and thick enamel buccally in both jaws. In the latest stage examined, a 48 mm CR *Bathyergus* fetus, no trace of dI1 was found in either jaw (see Table 1).

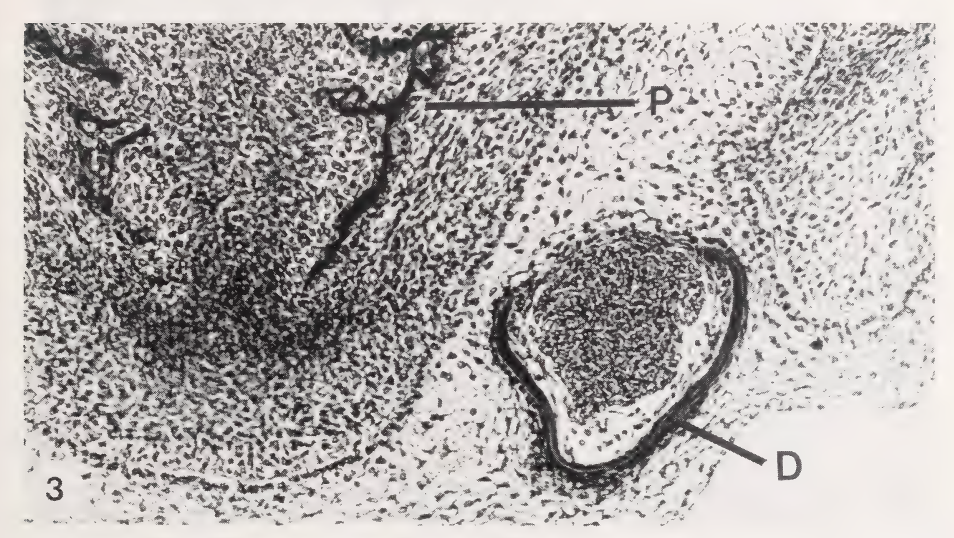


Fig. 3 Bathyergus janetta 21 mm CR fetus. Transverse section through upper jaw, showing the moderate-sized, abnormal dI1 projecting into the oral epithelium. A moderately-developed layer of dentin (D) is present, but there is no evidence of enamel, ameloblasts, or stellate reticulum. P = premaxillary bone trabeculae. (×400)

Family Ctenodactylidae

In a 15.5 mm CR fetus of *Ctenodactylus gundi,* a tiny nodular papilla, capped by a thin layer of dentin, projects into the basal surface of the oral epithelium in each jaw (see Table 1). As in *Bathyergus,* these abnormal dI1 lack stellate reticulum and a distinct separation between inner and outer enamel epithelia. The considerably larger dI2 are less differentiated, being in the early cap stage, but they exhibit normal relationships with the dental lamina and oral epithelium.

In later fetuses of 22, 32 and 41 mm CR, the tiny abnormal dI1 are represented by small dentinal knots, in which the irregular dentin exhibits varying degrees of fragmentation and partial resorption in both jaws (Fig. 4). In contrast, the large dI2 undergo normal differentiation of stellate reticulum, dentin and enamel during these stages (see Table 1).

Families Pedetidae and Anomaluridae

We have examined only a single fetus from each of these families to date (see Table 1), and we will describe them together. In a 24 mm CR fetus of *Pedetes caffer,* small, bell-shaped dI1 lie immediately beneath the oral epithelium and retain a broad connection to the latter. A thin layer of dentin covers the apex of the dental papilla, but odontoblasts are scattered within the dentin, rather than forming a distinct layer. The larger dI2 are less differentiated; they have only attained the late bud-early cap stage.

In a later fetus of *Anomalurops beecrofti* (44 mm CR), dI1 in each jaw consists of a tiny, abnormal dentinal cap (Fig. 5), which is partially resorbed at its basal surface. These teeth lie at the anterior ends of the jaws, immediately beneath the oral epithelium. Distal to this tooth lies the large, normal dI2, with thick dentin and moderately developed enamel on its buccal surface.

Discussion

The findings of the present study clearly indicate that the development of small, abnormal dI1 in both jaws is the "normal" or usual condition during early dental ontogeny in the African rodent families Bathyergidae and Ctenodactylidae, and probably also in Anomaluridae and Pedetidae. These observations provide additional corroboration for the hypothesis (Luckett 1985) that the presence of rudimentary dI1 during fetal life characterized the last common ancestor of extant rodents.

The developmental pattern of the abnormal dI1 and their relationships with the large, normal dI2 in bathyergids and ctenodactylids are similar in most respects with the condition described previously for sciurids (Luckett 1985). In these groups, the rudimentary teeth develop to the bell stage, but differ from normal teeth in that stellate reticulum does not differentiate during this stage. Concomitant with this, there is a lack of ameloblasts and enamel in later stages. Although the reasons are not completely understood, stellate reticulum appears to be necessary for the normal development of enamel in mammals. Another abnormal feature of rodent dI1 is the formation of an irregular dentinal knot, in which the odontoblasts become partially entrapped within the dentin, rather than forming a distinct odontoblastic layer. These abnormal attributes of rodent dI1 also characterize the developmental pattern of abnormal or vestigial deciduous teeth in a variety of other mammals (Moss-Salentijn 1978; Luckett and Maier 1982; Luckett and Zeller in press).

In contrast to the apparent consistent presence of small dI1 during early ontogeny in sciurids, bathyergids and ctenodactylids, they seem to be of more variable occurrence in muroid and caviomorph rodents. Thus, early studies (Freund 1892; Adloff 1898) failed to detect rudimentary dI1 in *Mus,* except in a single fetus described by Woodward (1894). However, a later study on a closely graded developmental series indicated that a tiny dI1 may be a normal constituent of the upper jaw during fetal and early postnatal life in *Mus* (Fitzgerald 1973). Moss-Salentijn (1978) has also reported the variable occurrence of rudimentary deciduous incisors in the rat. The distribution of these teeth in other muroids is unknown.

Despite numerous investigations of dental development in the South American caviomorph *Cavia* (Freund 1892; Adloff 1898; Tims 1901; Harman and Smith 1936; Berkovitz 1972), there appears to be only a single report of a possible rudimentary

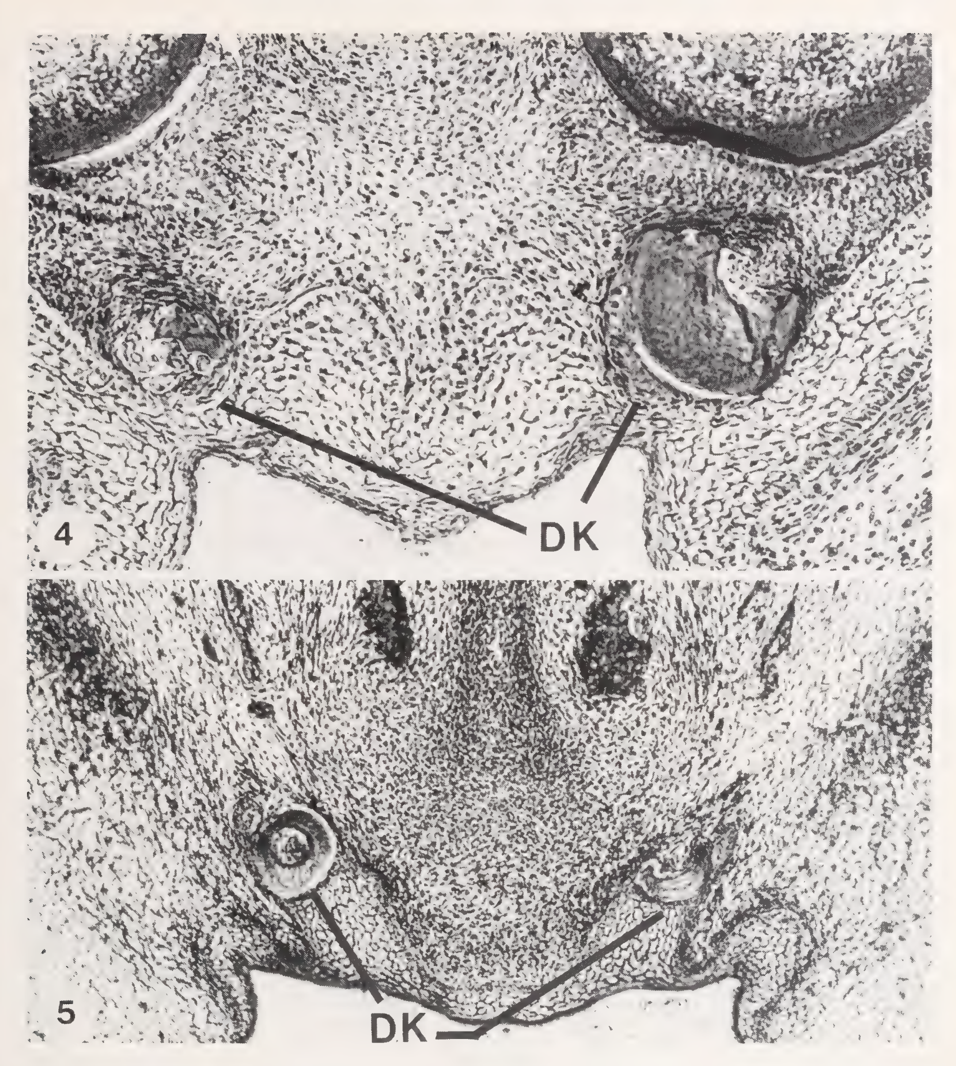


Fig. 4. Ctenodactylus gundi 41 mm CR fetus. Transverse section through upper jaw, showing the remnants of dI1 as tiny, partially resorbed, dentinal knots (DK). The tooth on the left side is almost completely resorbed. (×450). – *Fig. 5. Anomalurops beecrofti* 44 mm CR fetus. Transverse section through upper jaw, showing tiny, partially resorbed, dentinal knots (DK) of dI1 projecting into the oral epithelium. (×250)

deciduous incisor in this genus. Adloff (1898) believed that an early cap-like thickening in the lower jaw of a 30 mm head length (HL) fetus was homologous to the first deciduous incisor, although such a rudiment was absent in the upper jaw. In contrast, he found no trace of such a tooth in a younger 15 mm HL specimen, nor in a 40 mm HL *Dasyprocta* fetus. Until now, the only evidence for an unquestioned abnormal deciduous incisor in caviomorphs was the brief description and illustration of a tiny cap-like dentinal mass in both jaws of a single fetus of *Dactylomys* (family Echimyidae) by Muller (1927). Recently, we have prepared serial sections through a fetal head of the caviid *Galea musteloides* (27 mm CR; 14 mm HL), from the collection of the Zoology Department,

University of Tübingen. It possesses a small, well developed cap-like dentinal rudiment for dI_1 in the lower jaw, whereas only a condensed mass of connective tissue indicates the possible remnant of dI^1 in the upper jaw. Additional developmental stages of other caviomorph families should be investigated in order to determine the distribution of abnormal incisors in Caviomorpha.

The widespread occurrence of abnormal dI1 during ontogeny in rodent families suggests that these tooth germs may play an important functional role, despite their abnormal and transitory nature. If this is true, their functional activity is probably limited to the early phases of dental development in the fetus. Further understanding of the developmental interrelationships between oral ectoderm and migrating neural crest cells during the initial stages of dental lamina and tooth bud formation (Lumsden 1984) should provide additional insight into the ontogenetic and phylogenetic significance of abnormal deciduous incisors in rodents.

Acknowledgements

The authors gratefully acknowledge the use of material from the Embryological Collection of the Hubrecht Laboratory, Netherlands Institute for Developmental Biology, Utrecht, The Netherlands, through the aid of Dr. Gesineke Bangma, and from the Van der Horst Collection, Zoology Department, University of the Witwatersrand, Johannesburg, South Africa, through the aid of Dr. Robin Crewe (see Table 1). We thank Dr. Pierre Charles-Dominique, Brunoy, France, for donating the fetus of *Anomalurops*. The histological serial sections were skillfully prepared by Mrs. Klaudia Schrenk, and we thank Dr. Nancy Hong and Miss Uschi Trautmann for their photographic assistance. This study was supported in part by a Senior U. S. Scientist Award from the Alexander von Humboldt Foundation, Bonn, to the senior author.

Zusammenfassung

Über das Auftreten abnormaler Incisiven im Milchgebiß während der pränatalen Entwicklung bei afrikanischen „hystricomorphen" Rodentia

Frühe Stadien der Zahnentwicklung wurden in vier Familien und fünf Gattungen afrikanischer „hystricomorpher" Nager untersucht. Kleine, abnormale vordere Milchzähne (Incisiven, dI1) wurden sowohl im Oberkiefer als auch im Unterkiefer beobachtet. Sie treten rostral der großen, normalen dI2 in frühen Entwicklungsstadien aller untersuchten Arten auf *(Bathyergus janetta, Georychus capensis, Ctenodactylus gundi, Pedetes caffer* und *Anomalurops beecrofti).* Die kleinen abnormalen Zähne entwickeln einen unregelmäßigen Dentinkern, weisen jedoch weder Ameloblasten noch Schmelz auf. Ein ähnliches morphogenetisches Erscheinungsbild bieten die vorderen Milchzähne der Sciuriden, und es entspricht wahrscheinlich dem für Nager ursprünglichen Zustand. Die funktionelle Bedeutung dieser abnormalen Zähne in der Ontogenese ist bis jetzt unbekannt.

References

Adloff, P. (1898): Zur Entwicklungsgeschichte des Nagetiergebisses. Jena. Z. Naturw. **32**, 347–411.

Berkovitz, B. K. B. (1972): Ontogeny of tooth replacement in the guinea pig *(Cavia cobaya).* Archs. Oral Biol. **17**, 711–718.

Fitzgerald, L. R. (1973): Deciduous incisor teeth of the mouse *(Mus musculus).* Archs. Oral Biol. **18**, 381–389.

Freund, P. (1892): Beiträge zur Entwicklungsgeschichte der Zahnanlagen bei Nagetieren. Arch. mikr. Anat. **39**, 525–555.

Harman, M. T.; Smith, A. (1936): Some observations on the development of the teeth of *Cavia cobaya.* Anat. Rec. **66**, 97–111.

Heinick, P. (1908): Über die Entwicklung des Zahnsystems von *Castor fiber* L. Zool. Jahrb. Abt. Anat. **26**, 355–402.

Luckett, W. P. (1985): Superordinal and intraordinal affinities of rodents: developmental evidence from the dentition and placentation. In: Evolutionary Relationships among Rodents. Ed. by W. P. Luckett and J.-L. Hartenberger. New York: Plenum Press, 227–276.

Luckett, W. P.; Maier, W. (1982): Development of deciduous and permanent dentition in *Tarsius* and its phylogenetic significance. Folia Primatol. **37**, 1–36.

Luckett, W. P.; Zeller, U. (1988): Developmental evidence for premolar dental homologies in the monotreme *Ornithorhynchus* and its systematic implications. Z. Säugetierkunde (in press).

Lumsden, A. G. S. (1984): Tooth morphogenesis: contributions of the cranial neural crest in mammals. In: Morphogenèse et différenciation dentaires. Ed. by A. B. Belcourt and J.-V. Ruch. Paris: INSERM, Vol. **125**, 29–40.

Maier, W.; Schrenk, F. (1987): The hystricomorphy of the Bathyergidae, as determined from ontogenetic evidence. Z. Säugetierkunde **52**, 156–164.

Moss-Salentijn, L. (1978): Vestigial teeth in the rabbit, rat and mouse; their relationship to the problem of lacteal dentitions. In: Development, function and evolution of teeth. Ed. by P. M. Butler and K. A. Joysey. London: Academic Press, 13–29.

Muller, J. (1927): On the occurrence of vascularized enamel-organs. Proc. Kon. Akad. Wetens. Amsterdam **30**, 298–307.

Schrenk, F. (1988): Zur Schädelentwicklung von *Ctenodactylus gundi.* Cour. Forsch.-Inst. Senckenberg (in press).

Tims, H. W. M. (1901): Tooth-genesis in the Caviidae. J. Linn. Soc. (Zool.) **28**, 261–290.

Wood, A. E. (1985): The relationships, origin and dispersal of the hystricognathous rodents. In: Evolutionary relationships among rodents. Ed. by W. P. Luckett and J.-L. Hartenberger. New York: Plenum Press, 475–513.

Woodward, M. F. (1894): On the milk dentition of the Rodentia with a description of a vestigial milk incisor in the mouse *(Mus musculus).* Anat. Anz. **9**, 619–631.

Authors' addresses: Prof. Dr. W. Patrick Luckett, Department of Anatomy, University of Puerto Rico, Medical Sciences Campus, GPO Box 5067, San Juan, Puerto Rico 00936, USA; Dr. F. Schrenk and Prof. Dr. Wolfgang Maier, Institut für Biologie III, Lehrstuhl für Zoologie, Universität Tübingen, D-7400 Tübingen 1

Z. Säugetierkunde 54 (1989) 304–323

ISSN 0044-3468

The influence of food supply on the population dynamics of rabbits, *Oryctolagus cuniculus* (L.), in a Dutch dune area

By J. Marijke Wallage-Drees and Nora Croin Michielsen

Department of Population Biology, University of Leiden, Leiden, The Netherlands

Receipt of Ms. 24. 2. 1988

Abstract

The population dynamics of rabbits in a temperate, maritime climate were studied in response to the question: are rabbit numbers kept in check by intrinsic responses to density, or by predation and disease, or do they rise to the level permitted by the food supply? The study was carried out in a few small observation plots within a coastal dune nature reserve. An experiment employing supplemental feeding was conducted during autumn and winter. In the severe winter of 1978–79 rabbits died from starvation. In the following years population density increased, but did not reach the upper limit set by food availability. Fullgrown rabbits were eaten by fox, stoat and occasionally cat and polecat. Littering frequency was low and may have been depressed by high rabbit density. The length of the breeding season was determined by an interaction between population density and food quality. Predation and other mechanisms potentially capable of regulating population size were not strong enough to keep rabbit density below the level permitted by the food supply. Reasons for this are discussed.

Introduction

In the coastal sand dunes of the Netherlands many nature reserves are established. The vegetation is vulnerable to overgrazing, which can lead to rain and wind erosion. Rabbits can cause severe damage to dune vegetation, and in many places managers try to control rabbit populations by hunting them during autumn and winter. The question remains, however, whether availability of food during the winter already limits rabbit population densities. This question has become more of present interest since the impact of myxomatosis is lessening.

It has been discussed widely as to whether herbivore numbers are limited by food supply, or whether intrinsic behavioural responses to high density, or predation or disease, prevent populations from reaching the limit set by food availability.

Watson and Moss (1970) argued that since changes in behaviour (dominance, spacing behaviour and aggression) invariably attend population limitation, these factors must be all-important in setting population size. However, it is more likely that changes in behaviour arise as inevitable symptoms of cover-crowding displayed as the carrying capacity of the habitat is reached (e. g. Lack 1954).

Cowan and Garson (1985) describe how rabbit numbers are limited by the number of burrows on the chalk, but not on the dunes. On the chalk, much more aggression and burrow defence occurred.

Gibb et al. (1978) considered that density-dependent behavioural or physiological mechanisms were too weak to regulate populations of rabbits. They stated that "the population of rabbits appeared to be limited by extrinsic factors alone" and concluded that rabbit populations in New Zealand were kept in check by predators, mainly feral cats and ferrets.

Rabbits have been particularly well studied in Australia. Myers and Poole (1963) concluded that starvation was the only mortality factor of consequence in determining density. Myers (1971) forwards the hypothesis that the characteristics of rabbit population

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5405-0304 $ 02.50/0

dynamics in Australia reflect the conditions under which the rabbit originally evolved: "The rabbit in Australia possesses no inbuilt physiological or behavioural mechanism to control its numbers. The rabbit evolved in a system where extrinsic mortality factors (mainly predation) are necessary to maintain population stability."

The rabbit evolved in the Mediterranean region (FLUX and FULLAGAR 1983), and so, according to MYERS, rabbit numbers there should be kept in check by predation.

Compared with the relatively recent introductions of rabbits in Australia and New Zealand, rabbits have been established in north-western Europe since 1250 (RENTENAAR 1978; VAN DER FEEN 1963). Predation might be expected to have a greater impact on rabbit numbers in these older habitats. However, with regard to predation, the situation in north-west Europe is quite different from that in the Mediterranean. DELIBES and HIRALDO (1981) describe that in Spain many more birds of prey and mammalian predators prey on rabbits than in other parts of Europe.

Historically, foxes, cats, mustelids and birds of prey have been much hunted in the dutch coastal dunes, to protect hunting and commercial interests in rabbits. Predators are protected now, and the fox has re-established itself since 1968. This fact led to this study on the population dynamics of rabbits.

The study was set up to determine whether rabbit numbers rise to the level permitted by their food supply.

It is impossible to quantify food supply correctly. Standing vegetation is not the same as available food. Only part of the vegetation is usable, so suitable food can be in short supply even where vegetation is abundant (SINCLAIR 1975). In addition, rabbit grazing can effect the composition of vegetation and hence the suitability of the habitat, and plants may show compensatory growth in response to grazing (McNaughton 1983).

Therefore, to determine whether rabbit numbers have reached the level set by the food supply, we studied whether reproduction and survival are food-dependent.

A few small populations were monitored by catching, marking and observing over several years. By providing supplementary food to one population it could be determined whether relieving food scarcity in wintertime led to reduced mortality and an increase in reproduction.

This experimental approach was supplemented by a study on condition and diseases of rabbits shot in other parts of that same dune reserve (WALLAGE-DREES 1986).

Observations on rabbit breeding in stops was done on a former arable field used as parking lot in the same dune reserve.

Methods

The study area

The study was carried out between January 1978 and June 1981 in the 'Noord-Hollands Duinreservaat' (NHD), and area covering 4765 ha of coastal dunes northwest of Amsterdam. The reserve is managed by the Provincial Waterworks of North-Holland (PWN), and rabbits are hunted by game wardens in order to reduce damage. With their help many data on condition and food of rabbits were collected (WALLAGE-DREES 1986; WALLAGE-DREES and DEINUM 1986).

The actual study area was situated about 800 m from the sea in a vegetation mosaic of *Hippophaë rhamnoides, Rubus caesius, Salix repens*, mosses, forbs, grasses and sedges (mainly *Festuca ovina, Carex repens*) classified as '*Rubus caesius* landscape' (DOING 1964).

This coastal area has a mild, maritime climate (fig. 1) with little seasonal fluctuation in rainfall. There is usually some snow in January and February. The first study winter in 1979 was much colder than average; snow covered the ground completely for 23 days in January and February and there were at least 5 days with glazed frost.

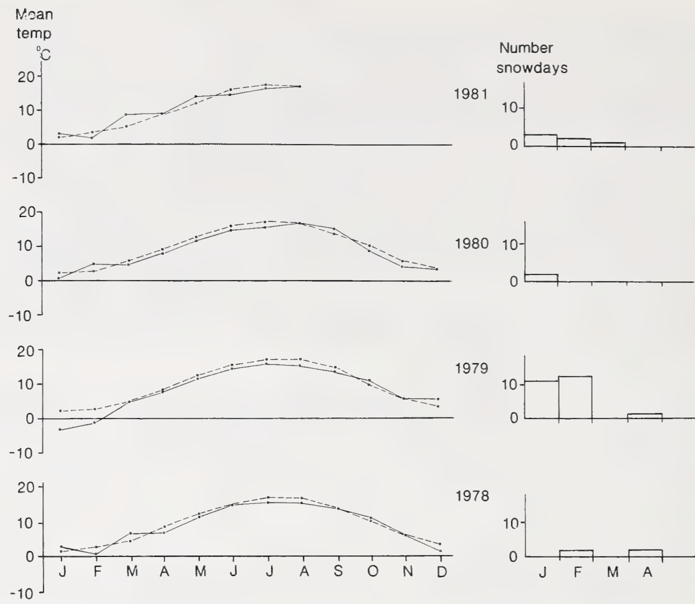


Fig. 1. Left: Monthly temperature means in °C (·—·) together with the means over 1950–1980 (·- - -·). Data from KNMI, De Bilt. – *Right:* Number of days with complete snow cover. Data from the recording station of PWN at Castricum

The observed populations

Rabbits were observed in seven plots (table 1). Five plots were made by fencing in a few inhabited burrow systems, including foraging areas, while the sixth and seventh populations were left as unfenced controls. Plot 7 was added in 1980 and was bounded on two sides by a canal, on a third side by high grass not used by the rabbits and was open on the fourth side.

The boundaries of plots 6 and 7 were determined from observations on the movements of the rabbits that lived inside the plots.

The size of our plots varied from 0.7 to 1.4 ha (table 1). Myers (1964) did not notice any detrimental effect on behaviour or physiology when keeping rabbits in enclosures of 0.3 and 0.7 ha.

Fences were 1 m high with a mesh width of 3 cm. They were designed to ensure which rabbits got the supplemental food, while (as far as possible) allowing free access to predators.

Table 1. **Size of the plots in the study area**

Fenced				Unfenced		
No.	Size	In use		No.	Size	In use
1	1.3 ha	1978–79		6	1.3 ha	1978–79
2	0.7 ha	1978–79,	1980–81	7	1.4 ha	1979–81
3	0.7 ha	1978–79				
4	1.3 ha	1978–79				
5[1]	1.4 ha	1978–79,	1980–81			

[1] Plot with supplementary feeding.

The drawback of fencing was that it prevented dispersal. However, dispersal in rabbits is generally found to be small and not responsible for regulating population density (Gibb 1977; Myers and Poole 1961; Myers and Schneider 1964; Mykytowycz and Gambale 1965; Southern 1940; Tyndale-Biscoe and Williams 1955). We never noticed immigration of untagged rabbits into our unfenced populations and consequently, also considered that there was no emigration. This was

corroborated by the fact that no tagged rabbits from the observed populations were seen or shot outside the study are. Also, from rabbits tagged as nest young on the parking lot, 5 out of 45 were shot in their first year, all not farther than the border of the parking lot.

We believe that fences did not significantly influence predator activity. The main predators in the coastal dunes were stoat, polecat, fox and feral cat. Both stoat and polecat could creep through the fence and cats and foxes could climb over it. From tracks and sightings we know that stoats, polecats and foxes got inside the fences.

The fences possibly increased the chance of predation by making escape more difficult. This could only be checked for predation by stoats. Predation by a stoat can be recognized from bite-wounds on the rear of the animal (only visible by removing the fur), a gaping wound in the neck, and extensive subcutaneous haemorrhage (Hewson and Healing 1971). The fenced plots and another similar area of the same size (5.4 ha) were searched for rabbit carcasses. Between 1 November 1978 and 1 March 79, 14 carcasses/ha were found in the fenced areas and the same number in the searched area. Therefore, assuming the same population density on both sites, fences do not seem to have influenced the level of mortality caused by stoats.

Parameters of survival and reproduction

Two sets of parameters were measured. Population size in autumn and winter, impact of predation, body weight in wintertime were assessed with regard to rabbit survival and litter size, timing of the breeding season, littering rate, growth and survival of the young, the relative participation of adult and juvenile females in breeding were assessed with regard to reproduction.

Supplemental feeding experiment

To determine the influence of food availability on winter mortality an experiment was conducted in which the rabbits in plot no. 5 were supplied with additional food. This consisted of oats, wheat and the peel of *Ceratonia siliqua,* producing a mixture of high energy and low protein. Food was scattered ad libitum every two days at three foraging spots from 21 October 1980 until 20 March 1981. The food remained in good condition for at least two days. If little food was left over, the amount supplied was increased. Initially, 2.25 kg was given at each feed, which was increased to 4.5 kg from December onwards.

Condition of rabbits and population size

Rabbits were caught in live traps baited with oats and set at foraging spots. A few were caught by ferreting. After capture weight, sex and length of the hindfoot were recorded. Because rabbits were released we used body weight to distinguish juvenile(first-year) and adult rabbits. In shot rabbits from the same reserve body weight correlated well with eyelens weight, which is regarded as a reliable parameter of age (Wallage-Drees 1986). To determine whether females were pregnant and/or suckling, the condition of the nipples and the fur on the belly were checked (females line the nest with fur shortly before parturition) and the belly palpated. At first capture, rabbits were marked on both ears with a label that could be recognized at day or night when observing with a telescope: a monel wing band size 4 with an enlarged surface covered with reflecting yellow tape and with an individual code in black letters and numbers.

Two methods were used for estimating population size:

a. Field counts were made just after sunset. The highest value of four counts on consecutive days was divided by the maximum proportion that was above ground in the same area during that month (Wallage-Drees 1988).
b. From September 1979 onwards, when the major part of the population had been marked, live-calenders were constructed from recaptures and sighting. The number of unmarked individuals was assessed from sightings.

Population size was not calculated using a capture-recapture method, however, because the chances of being caught were not randomly distributed (Daly 1981; this paper table 2).

The whole observation area was searched intensively during the study and the chances of having missed emergent litters or fullgrown rabbits with severe myxomatosis were low. Also, the game wardens were aware of our study and brought us tags or tagged rabbits whenever they found them.

Recruitment and juvenile survival

Young rabbits are born in a nest-chamber, either in a blind diverticulum of a warren system or at the end of a separate blind tunnel called a 'stop' (Lloyd and Cowan 1968). The doe visits the young only once or twice during 24 hours and leaves the nesting burrow blocked up while she is absent. Young

rabbits emerge and make small excursions outside the burrow from about their 22nd day (Broekhuizen et al. 1986). From that age onward they could be caught in traps set in the burrow entrance. The probability of capturing them was increased by finding the places where young emerged. Older young were also caught in traps set at foraging spots. Young were marked with the same tags as the adults.

The populations under observation littered in existing burrows. Many nests appeared to be located in empty burrows of which there were large numbers.

Stops were found on former arable fields in the reserve, which are now used as parking lots or as playgrounds. Nests in stops provided data on litter size and growth of kittens that could not be obtained from the actual study area.

Litter size is affected by the partial loss of embryos during gestation (Brambell 1943) and by the death of part of the litter in the nest. One has to be careful in opening a stop lest the doe deserts the young. We found that stops with young under 10 days, even when opened carefully and blocked again after inspection, were deserted by the mother. The birth date was estimated from the timing of visits by the doe: once the young are born she opens the stop every night (Myers 1958). Litter size was defined as the size at the first count 10 days after the birth of the litter.

In 1980 und '81 not enough stops were found to determine litter size from nests in stops. However, in 1981, the litter size in utero from rabbits shot in February and March could be recorded when uterine swellings were visible at dissection. The embryos were aged according to the drawings of Minot and Taylor (1905).

Littering rate

The littering rate is the number of litters born each month divided by the number of adult females present at the beginning of the next month (Parer 1977). In this study the number of litters per year per doe was assessed by observation and capture of emergent young.

Rabbits have a post-partum oestrus. In this study littering rate was never 100 %. No distinction could be made between does that did not conceive post-partum, lost embryos before full-term, or whose young did not survive till emergence.

Pattern of the breeding season

The pattern of the breeding season was deduced from the appearance of litters in the study area and the distribution of age cohorts in the autumn bag of the wardens.

The age of dead rabbits

The age of dead rabbits was determined using their eyelens weight according to the formula given by Myers and Gilbert (1968), i. e. age (days) = −57 + 181.4/ln(314/lens weight [mg]). A similar formula was found in this study, based on data from 15 rabbits with known birth date who were either shot at the parking lot or found dead in the study area. This sample gave: age (days) = −64+228.8/ln(314/lens weight [mg]) which lies within the 11 % standard deviation given by Myers and Gilbert (1968). As their formula was based on a much larger sample, it was used.

Available food in the breeding season

To assess the quantity and quality of food available during the breeding season, the relative biomass of the vegetation was measured from mid-February to mid-June. The relative biomass of a 'species' was defined as the product of cover and average height. Cover was measured by the point-quadrat method (Mueller-Dombois and Ellenberg 1974) and average height by measuring all plants touching the point quadrat within a distance of 0.5 cm. This was done on a grid of 392 points. Cover was summed and height averaged for monocotyledons and dicotyledons separately, as these show a difference in quality as rabbit food (Wallage-Drees 1983).

Results

Winter mortality

Capture rate

Captures in the baited live-traps were not distributed at random with regard to age and sex. For example, table 2 gives figures for a few months in which the composition of the population was well-known. In autumn juveniles were caught more often than adults (2A), pregnant does were caught more often than bucks (2B) and supplementary feeding reduced the chance of capture (2C). In September, juveniles increased in weight more than adults (table 7), and does need extra food when pregnant or lactating. Generally, one might conclude that rabbits which need more food enter the traps more readily.

Table 2. **Capture rates**

A Frequency of captures of adults and juveniles plot 2 and 7

	September 1980			January 1981		
	n	captures	χ^2	n	captures	χ^2
Adults	36	3	85.3 ($p < 0.001$)	8	6	0.76 n.s.
Juveniles	12	33		17	8	

B Frequency of captures of ♂♂ or ♀♀ in the reproductive season (1 March–3 June) 1981, plots 2, 5 and 7

	n	captures	χ^2
♂♂	14	17	11.9 ($p < 0.001$)
♀♀	18	55	

C Frequency of captures in plot 5 with supplementary feeding, compared with the untreated plots 2 and 7 (January 1981)

	n	captures	χ^2
Plot 5	16	3	3.3 n.s.
Plots 2 and 7	25	14	

Tested: observed vs. expected values.
n = population size.

Population reduction

Table 3 gives the number of rabbits in the plots and the mortality rate during autumn and winter. A variable number of plots were used, because, following heavy mortality in the winter of 1978–79, not enough rabbits survived in the original study area to continue the work there. Consequently, we moved to another area nearby called plot 7. Meanwhile, plots 2 and 5 were restocked with rabbits caught in other parts of the reserve, and so plots 2,5 and 7 could be monitored in 1980–'81. The mortality rate varied between months and years. It was highest from December 1978 to March 1979. In 1980–81 no differences in mortality rate were found between plot 5, with supplemental feeding, and the controls.

For 1979–80 and 1980–81 the mortality of juveniles and adults and of the two sexes were calculated separately. No significant differences were found, either between age-groups or sexes, and therefore, these classes are not treated separately in table 3.

Table 3. **Population size and mortality in the study areas**

	Population size			Mortality (%)	
	Sept.	Dec.	March	Sept.–Dec	Dec.–March
1978–'79					
Plot 1–6	244	89	25	64	72
6.7 ha					
1979–'80					
Plot 7	41	32	21	22	34
1.4 ha					
1980–'81					
Plots 2 and 7	48	29	19	40	34
2.1 ha					
Plots 5[1]					
1.4 ha	29	21	12	28	43

Population decrease 1978–79 vs. 1979–80: $\varkappa^2 = 40.6$ $p < 0.001$
1980–81: $\varkappa^2 = 24.7$ $p < 0.001$
Population decrease 1979–80 vs. 1980–81: $\varkappa^2 = 0.79$ n.s.
1980–81, in autumn, plot 5 vs. plot 2 and 7: $\varkappa^2 = 0.68$ n.s.
1980–81, in winter, plot 5 vs. plot 2 and 7: $\varkappa^2 = 0.09$ n.s.

[1] Experimental plot: supplemental feeding during October to March.

Causes of death

In table 4 data about the causes of death are summarized and compared to the decrease in total population numbers. The decrease in population numbers shows that the number of rabbits that disappeared without their carcasses being found was higher in autumn 1978 than in winter 1978–79. This was due on the one hand to the lower rate of decay in winter and on the other hand to our attention being drawn to the carcasses by the behaviour of magpies, who were more attracted to carcasses in winter than in autumn.

First, we examine whether the catching procedure caused additional mortality. During

Table 4. **Number of rabbits that died and causes of death**

	a	b	c	d	e	f	g
1978–79 (6,7 ha)							
Sept.–Oct.	44	0	0	3	1	9	31
Oct.–Nov.	93	0	1	17	0	2	73
Nov.–Dec. }	46	1	1	20	0	1 }	15
Dec.–Jan. }		0	1	5	0	2 }	
Jan.–Feb.	24	1	0	19	0	2	2
Feb.–March	22	2	0	8	1	11	0
1980–81* (3,5 ha)							
Sept.–Oct.	3	1	1	0	0	0	1
Oct.–Nov.	12	1	0	0	0	0	11
Nov.–Dec.	12	1	0	0	0	0	11
Dec.–Jan.	9	0	0	0	0	2	7
Jan.–Feb.	6	0	0	0	0	0	6
Feb.–March	4	1	0	0	0	0	3

* 1979–80 (no carcasses or remains found).
a = estimated total number of deaths at the study site, b = trap or ferret, c = myxomatosis, d = stoat, e = fox, f = carcass found, cause unidentified, g = a–(b to f) missing.

the three years of the study 9 rabbits were found dead in traps (table 5). From the study of the warden's game bag we know that the lethal minimum body weight of adults is around 1100 g (Wallage-Drees 1986: fig. 5). Therefore, we expect that rabbits of about this weight or less, if they had not been caught in a trap, would have died from starvation. In two cases, two rabbits were found together in the same trap. This could have been responsible for the death of one of them, but because of the small number involved, this was only a minor addition to deaths from natural causes.

Table 5. **Rabbits found dead in live-traps 1978–1981**

Date	Body weight (g)	Comments
2–03–1978	860	
9–02–1979	1225	myxomatosis
23–02–1979	1150	
23–02–1979	1100	
21–03–1979	890	
16–09–1980	930	2 rabbits in one trap, one dead
13–11–1980	950	
3–03–1981	1280	2 rabbits in one trap, one dead
03–04–1981	1380	weight loss 240 g since 15–03

Diseases and parasites

Rabbits caught in live-traps did not manifest any symptoms of disease, except for myxomatosis. Rabbits shot in another part of the reserve and dissected had intestinal parasites, especially *Graphidium strigosum* and *Taenia* sp. These rabbits did, however, seem to be in good condition. Only one out of 175 rabbits showed symptoms of liver coccidiosis.

Few rabbits with symptoms of myxomatosis were found (table 4). Other evidence also indicated a low rate of mortality from myxomatosis. Over the three years of the study, 29 animals on the study site were seen to have myxomatosis: 23 of these were juveniles and 6 were adults. At least 10 of the rabbits are known to have recovered. Myxomatosis occurred mainly at the end of summer (table 6). Nestlings may die from myxomatosis in spring without showing symptoms (Fenner and Ratcliffe 1965). In this study causes of death of nestlings were not assessed.

Table 6. **Number of rabbits on the study site seen with myxomatosis**

	1978–79	1979–80	1980–81
September	7	0	1
October	2	0	0
November	2	0	0
December	1	0	0
January	0	0	1
February	0	0	0
March	0	0	0
April	0	1	1
May	0	1	1
June	0	1	–
July	1	3	–
August	0	6	–

Starvation

The chance of capture was higher in rabbits that required more food (table 2). Therefore, if there had been starving rabbits in the study area, they should have been caught. In the winter of 1978–79 three of the 'trap deaths' could be attributed to starvation. In this year we observed that rabbits were less alert: another sign of starvation.

In 1980–81 we did not see any evidence of starvation. The weight changes of ten rabbits that disappeared during December-February, and were assumed to have died, were known up to the time of disappearance. These had all been positive (+0.66 to +5.66 g/day). The

comparable figure for rabbits who were observed to be alive in March was −1.10 to +5.40 g/day, (n = 13). This does not suggest that starvation was a cause of mortality in this year.

Predation

Predation is almost always elusive and hard to measure. The number of rabbits caught by predators can only partly be deduced from table 4. Full-grown rabbits in the coastal dunes were eaten by fox, polecat, stoat and feral cat, and the first three species were seen in the study area. Large numbers of rabbits killed by stoats were found in 1978–79 (table 4, column d). In addition, many of the carcasses of which the condition did not allow determination of the cause of death (table 4, column f) may also have been killed by stoat. Magpies often found the carcass and ate what was left.

In November and December 1978 we found 15 juvenile rabbits killed by stoats that had not yet been damaged by magpies. Their mean weight (± s. e.) was 1380 ± 45 g. When we simulated the wounds to rabbits caused by stoats we concluded that an average of 40 g of flesh were eaten. Adding this eaten part gives a converted mean weight of the juvenile rabbits of 1420 g. The mean weight of juveniles in the warden's game bag for the same months was 1450 g ± 25 (n = 64). During this period only one adult rabbit was found killed by a stoat. This suggests that stoats take healthy, but inexperienced rabbits. Stoats may have had no other choice, however, because there were no weakened rabbits present at this time of year. By taking healthy prey the stoat could be a factor influencing rabbit population density.

Polecat kills were not found, but may have been included in the figures for the stoat. A polecat might drag a full-grown rabbit away from the spot where it was caught, but only in the unfenced plots. The same applies to the cats and foxes. Feral cats were scarce in the Dune Reserve. Foxes are known to carry away their prey and bury it, so reducing the chance of finding the remains of fox kills. Carcasses with the head severed or buried were attributed to foxes. Such prey remains were found only twice during the study (table 4, column e).

The number of rabbits caught by foxes were be assessed in the following way. Mulder (1985b), who studied the fox in the same dune reserve, estimated that rabbits constitute 90 % of the weight of the diet of foxes. A fox needs 350–550 g (Lloyd 1980) to 480–700 g (Niewold 1976) of food per day. An average (juvenile) rabbit weighed around 1500 g (Wallage-Drees 1986). Therefore, one rabbit and some other prey may provide a fox with food for two days. Fox territories in the NHD, on average, covered 165 ha and contained three adult foxes and their young at years of high fox population density. In 1980 they usually contained two adults. Here we calculate the situation at maximum fox density. Assuming that from September until December three adult and three full-sized young inhabit a territory, and that from 1 December the young start to disperse, we might expect 6 foxes/165 ha from September through November and 4 foxes/165 ha from December through April (Mulder 1985a). Their minimum food requirement would then be: 90 rabbits/165 ha per month during Sept.–Nov., and 60 rabbits/165 ha per month during Dec.–April. They might waste food in autumn, but it was assumed not in winter.

Foxes were expected, therefore, to remove one or two rabbits per month over the whole of the three plots of the study in 1980–81; a small loss compared to total rabbit numbers at that time (table 3).

During the study period there was a change in the populations of predators. From spring 1979 onwards, stoats became rare in the whole dune reserve. Foxes have lived in the Reserve since 1968. Their numbers increased up to 1981, after which they remained constant (J. L. Mulder pers. comm.). The increase of the fox population may explain why so few rabbit carcasses were found after spring 1979 (table 4): foxes eat carcasses as well as live prey and both types of food are carried away and hidden.

The impact of the stoat was quite high during the winter of 1978–79. Rabbits weakened by food shortage might have been more susceptible to predation, but the apparently greater effect could have been due partly to the fact that we noticed the carcasses sooner in winter than in the autumn.

With the fall in stoat numbers in spring 1979, predation pressure on rabbits decreased.

The experiment with supplemental feeding

In 1980–81, rabbits in plot 5 were given additional food, but this did not reduce winter mortality (table 3).

Table 7 gives the change in body weight of rabbits that were caught at least twice. In plot no. 5 both adults and juveniles showed a weight gain during autumn and winter, but in the untreated plots, adults lost weight over both periods, and juveniles only gained weight during autumn. All differences between treated and untreated plots were significant, even for the juveniles in autumn. Juveniles supplied with extra food gained more weight than did juveniles in the untreated plots.

One effect of supplemental feeding was that young were born in this population weeks ahead of the usual start of the reproductive season (WALLAGE-DREES 1983). Only three of them emerged, apparently because the conditions in February and March are too harsh for nestlings or suckling does. The ones that emerged had a low growth rate (table 10).

Table 7. **Change in body weight in control plots, and in populations supplemented with food (g/day ± s.e.)**

	n	1 Sept.–30. Dec. 1980	n	15 Dec. 1980–6 March 1981
Adults plot 2, 6 and 7	5	-1.3 ± 1.6	4	-1.7 ± 0.8
Adults plot 5[1]	5	$+3.5 \pm 0.9$	0	
	$t = 3.78$, $p < 0.05$			
Juv. plot 2, 6 and 7	12	$+2.8 \pm 0.1$	6	-0.9 ± 1.2
Juv. plot 5[+]	8	$+3.6 \pm 0.4$	4	$+4.9 \pm 2.3$
	$t = 4.42$, $p < 0.05$			

[1] Experimental plot: supplementary feeding during October–March.
n = number of rabbits that were caught twice or more in the period.

Productivity

Litter size

The factors which contribute most to a high rate of population increase are early maturation, large litter size, high littering rate and high survival rate of the young.

In 1978 the mean litter size of 34 litters in stops was 5.0 ± 0.2. Litter size increased from spring to summer (fig. 2) as described by the regression equation for March 21 to May 17: $Y = -0.4 + 0.05X$, $r = 0.478$, $p < 0.005$, where Y is the litter size and X is the birth date as day of the year.

In 1979, 10 stops were found before June. The correlation of litter size with time was not significant. Litter sizes were smaller in 1979: mean litter size was 4.1 with a mean birth date of April 24. On that date the expected litter size for 1978 would have been 5.3.

In 1980 und 1981 three and zero stops were found, respectively, thus mean litter size could not be determined. The mean litter size in utero from 10 rabbits shot in February and March 1981, with an expected mean birth date of about April 1, was 4.4. This was in the range expected from the regression formula for 1978.

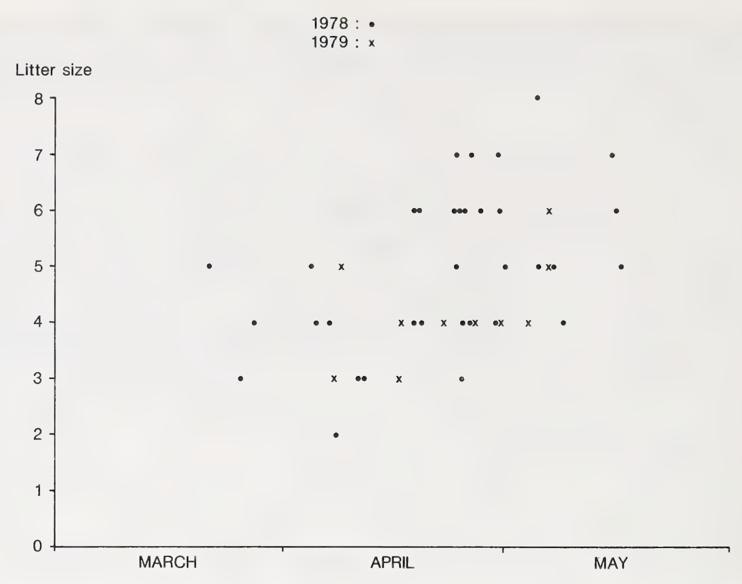


Fig. 2. Litter size in 1978 (●) and 1979 (×). From litters in stops on a parking lot in the dune reserve

Littering rate and length of the breeding season

Fig. 3 shows the birth dates of litters during the study. Data from plot 5 with supplemental feeding are excluded from this figure. In 1978, young from 27 litters were seen in the study plots, compared to an estimated number of 25 adult does, giving littering rates of 36 % in April, 44 % in May and 20 % in June.

It was not possible to gather similar data in 1979, due to the scarcity of rabbits. In 1980 the birth dates of individual young caught in traps was determined.

In 1981, observations ended in June, so only the first part of the breeding season was recorded. Eight adult does were estimated to be present in the study in this year, giving littering rates for March of 50 % and April of 88 %.

Generally the main breeding season was confined to March, April and May, with a smaller number of litters produced into August.

In 1979, due to the high mortality in the preceding winter, there were not enough rabbits in the study area to assess the pattern of breeding from observation and capture of young. To compare the length and pattern of the breeding season between years, the frequency of occurrence of young of different age cohorts (born in different months of the year) in the game bag were determined (table 8). This showed that the peak of the frequency distribution of births was later in 1979 than in 1978 or 1980.

Another indication for the fact that the breeding season lasted longer in 1979 was that in this year alone lactating does were among the rabbits shot in September (14 out of 20 adult ♀♀, and 2 out of 85 juvenile ♀♀, Fisher exact probability test for 1979 vs. 1978 + 1980: $p = 0.0003$).

The extended breeding season in 1979 did not compensate fully for the late start and smaller litter size. Overall, fewer young were born per doe in 1979 compared to the other years. In September 1979 the proportion of juveniles in the study area was 39 % (total $n = 41$), in September 1980 it was 69 % (total $n = 71$).

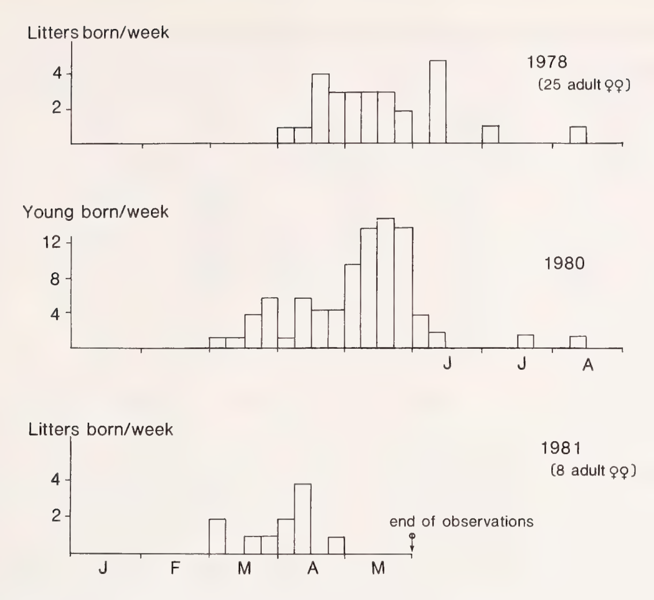


Fig. 3. Number of litters or young born per week in the study area

Table 8. **Frequency of age cohorts of juveniles in the game bag in 1978, 1979 and 1980**
Totals of September plus October

Month of birth	1978	1979	1980
June	7	45	13
May	27	69	41
April	53	70	36
March	28	16	25
February	8	4	10

Two-sample test Kolmogorov-Smirnov
1978 vs. 1979 D = 0.283 $p_2 \ll 0.001$
1979 vs. 1980 D = 0.182 $0.001 < p_2 < 0.01$
1978 vs. 1980 D = 0.156 $p_2 = 0.05$

Development of the vegetation

The availability of food during the breeding season is shown by the height and cover of the two main plant groups (table 9). The quantity of plant material increased from 1 March, and then decreased before mid-June, particularly in the quantity of dicotyledons which offer the best quality food. As the average height of the plants continued to increase over this period, this decrease seems not to have been caused by rabbit grazing.

Growth rate

The weight of young rabbits caught more than once were plotted against time. For nestlings and young from 200 to 1000 g the increase in weight was arithmetic (table 10). A relationship using the logistic form of the equation failed to improve the correlation. The

Table 9. **Relative biomass of the vegetation during the breeding season 1980**

Date	Dicotyledons Cover	Dicotyledons Height (mm)	Dicotyledons c×h	Monocotyledons Cover	Monocotyledons Height (mm)	Monocotyledons c×h
13 Feb.	0.10	12	1.20	0.71	19	13.49
27 Feb.	0.14	8	1.12	0.83	17	14.11
10 March	0.11	8	0.88	0.83	22	18.26
24 March	0.13	9	1.17	0.84	22	18.48
7 April	0.15	8	1.20	0.95	22	20.90
21 April	0.24	17	4.08	0.96	18	17.28
11 June	0.02	22	0.44	0.63	19	11.97

c×h = relative biomass.

Table 10. **Growth curves of young rabbits**

A. Growth curve of nestlings between day 10 and 21 1978 only
BW = 22.3 + 8.9 t, n = 15, r = 0.94

B. Growth curve of young between day 21 and 93
BW = 42.5 + GRt

year	n	GR	r
1978	18	10.0–11.2	0.98
1979	–		
1980	26	9.4– 9.8	0.99
1981 born in the usual season	47	8.6– 9.0	0.98
1981 born in Jan. in plot 5	3	7.6– 8.4	0.80

n = number of individuals that were caught repeatedly and weighed, BW = bodyweight in gramms, GR = 95 % confidence interval of the linear growth rate in g/day, t = age in days, r = correlation coefficient

growth rates found in this study are within the range of growth rates reported in other studies (table 11). Those from the young in the population receiving supplemental food that were born in January, much earlier than usual, were comparatively low.

Survival

The survival of young in different cohorts (born in different months of the year) was assessed from the composition of the game bag. Table 12 gives the frequencies of occurrence of age cohorts in the game bag and in the study site as a whole. In 1980–81 there was no significant difference in survival rate between young born early (i. e. March–May) or late in the season (i. e. June–July).

Table 11. **Growth rates in different countries**

Country	Author	Growth rate (g/day)
England	Southern (1940)	9.6
New Zealand	Tyndale-Biscoe and Williams (1955)	10
Australia	Dudszinski and Mykytowycz (1960)	6–11
	Dunnet (1956)	9.8
	Dunsmore (1971)	8–10
	Myers (1964)	10–11
	Myers and Poole (1963)	10–12
	Parer (1977)	10
	Parer and Fullagar (1986)	9.1
	Wheeler and King (1985)	10.5
	Wood (1980)	9.6–10.5

Table 12. **Survival rate of young born in different months**

12A. Frequency of age cohorts (young with different months of birth) in the monthly game bag of 1979

Lens weight mg	Sept. Cohort	n	Oct. Cohort	n	Nov. Cohort	n	Dec. Cohort	n
92–114	June	33						
115–132	May	54	June	12				
133–147	April	47	May	15	June	3		
148–160	March	9	April	23	May	5	June	4
161–172			March	7	April	7	May	17
173–182			Feb.	4	March	9	April	11
183–190							March	7
Total n		143		61		24		39

June cohort shot in September vs. june cohort in December:

$\varkappa^2 = 2.37$ n.s.

Young up to 3 months seldom appear in the game bag (Myers 1971). The July and August cohorts that appeared in October, November and December are neglected.

12B. Survival of age cohorts in the study area 1980–'81, plot 2, 6 and 7

Month of birth	n in Sept. 1980	Survival (%) till March 1981
March	5	20
April	14	36
May	7	29
June	0	
July	5	20
August	0	

Fisher exact probability test for March + April + May vs. June + July + August: p = 0.54, n.s.

Discussion

Population density

Occurrence of food shortage in autumn and winter

In the field it was impossible to assess the cause of death for every individual. It is assumed here that rabbits that were not seen again or recaught at the site any more had either died from disease or starvation inside the burrow, or had been carried away after predation.

There were no indications of diseases imparing survival, except for some myxomatosis in August and September during each year. Myxomatosis manifests itself only in spring and autumn and is no longer a major factor in determining the number of rabbits.

Evidence of the influence of food shortage on mortality was gathered in several ways: by assessing the condition of rabbits in wintertime (described in Wallage-Drees 1986), by assessing the quality of the available food in winter (Wallage-Drees and Deinum 1987) and by providing supplemental food (this study).

The condition of the rabbits in the study area was assessed by examining live rabbits caught in traps (table 7) and rabbits shot in the dune reserve outside the study area (Wallage-Drees 1986). Both data sets showed the same pattern: in all winters there was a decrease in weight, especially among juveniles. Only in the cold winter of 1978–79,

however, starvation did occur. In the other winters very few individuals showed signs of starvation.

Wallage-Drees and Deinum (1987) showed that from December 1980 till March 1981 digestibility of the food was below the maintenance level.

Supplemental food given to one fenced-in population in 1980–81 did not change the mortality rate. This indicates that mortality rate in years with 'normal' weather was determined by causes other than food shortage.

It should be realized that the level of the food supply itself is not constant. It changes stochastically with the weather and is influenced by the actions of rabbits, who deplete it at high density, but on the other hand increase its quality by promoting dicotyledons through their grazing (Gillham 1955).

During the study widely different weather conditions occurred. High mortality in the long winter of 1978–79 reduced numbers to a low level. In the following years, population density increased, but did not return to the pre-1979 level (table 3). Nevertheless, in 1980–81 a decrease in mean weight occurred in winter and the quality of the food was low.

Predation in autumn and winter

Gibb et al. (1978) found that rabbits in New Zealand hardly ever experienced food shortage because predators kept their numbers below the food limit. We will discuss under what circumstances predators have this impact on rabbits, and whether these are present here.

For vertebrate predators the following characteristics of the ecosystem are mentioned (Erlinge et al. 1983):

a. a rich supply of alternative prey sustaining a high and constant predator density. For example for foxes in Sweden, Erlinge et al. (1983) say that "their diet contained a high proportion of voles in autumn-winter and a low proportion in summer".
b. availability of prey for most of the year. Gibb et al. (1969) mention a year-round breeding and hence year-round availability of young rabbits.
c. a heterogeneous environment where the prey moves through habitats less suitable for them where they are vulnerable to predators (Wolff 1980).

Gibb et al. (1969) consider characteristic (b) combined with an effective predator like the cat to be sufficient explanation for regulation of rabbit numbers below the food limit.

The main predators in the coastal dunes were the stoat and the fox. Feral cats were rare. The change in the predator population, from stoat plus fox to fox only, occurred at about spring/summer 1979. The decrease of the stoat population could be due to food competition with the fox, especially in the early spring of 1979, when the number of rabbits was low. Also, direct predation by fox on stoat may be involved (cf. Erlinge 1983).

The decrease in stoat numbers led to lower predation pressure on rabbits. The number of rabbits/ha estimated to be taken by foxes was lower than the number taken by stoats (table 4). Stoats take only healthy animals, foxes both healthy and diseased ones (J. L. Mulder, pers. comm.).

Foxes behave as generalists, even though in the dunes rabbits were their main food. Their numbers are regulated by territorial behaviour and the density of breeding vixens is similar from year to year (Erlinge et al. 1983; Schantz 1984; J. L. Mulder, pers. comm.).

It is not the absolute number killed but the mortality rate inflicted when the prey population cannot compensate by lowering mortality rate from other causes, in this case the food supply, that is important for the impact of a predator on the dynamics of its prey. So, mortality in late winter has the largest impact (Errington 1946; Nicholson 1954; Solomon 1969). The 1 rabbit/ha per month taken by foxes in February could have some influence on a population density of about 7 rabbits/ha (table 3).

Looking again at the characteristics mentioned before

ad a.: foxes apparently hardly take any alternative prey in the coastal dunes.
ad b.: there is a short breeding season on the rabbit, young rabbits are only available from mid April–September.
ad c.: it seems that the whole dune system can be considered a refuge or optimal habitat for rabbits in the sense meant by WOLFF (1980). There is no suboptimal habitat whereto rabbits disperse at high densities.

In conclusion, in this study rabbit numbers grew to the point where they were limited by food and predation did not regulate rabbit numbers.

Recruitment

Intrinsic factors: influence of density on recruitment

Average litter size was 5, which was within the range expected in high-density populations (LLOYD 1970). Litter size is strongly related to body weight of the does (BRAMBELL 1943; POOLE 1960). The lower body weight of the does in this study in 1979 explains the smaller litter size in this year.

The low littering rate found in this study seems to be related to population density: it was higher in 1980 than in 1978.

The short breeding season in the study populations can be interpreted as an intrinsic response to high population density or as a response to low food quality in summer.

The beginning of the breeding season (presence of pregnant females) in February or March is determined by the availability of good quality food (WALLAGE-DREES 1983).

What determines the end of the breeding season? Usually the end is near 1 May. After that date few females become pregnant any more. For an explanation for the timing of the end of the breeding season we may consider the fact that there was a difference in the ending of reproduction between 1979, when reproduction continued or was resumed in summer, and 1978 and '80 when reproduction finished earlier.

Many authors from different countries in the northern and southern hemispheres mention that rabbits show a depression in fertility before or at summer solstice, with sometimes resumed breeding in autumn. They consider this an adaptation to arid conditions in the ancestral mediterranean homelands of the rabbit (BRAMBELL 1943; HUGHES and ROWLEY 1966; LLOYD 1970; MCILWAINE 1962; PARER 1977; POOLE 1960; ROGERS 1981; SORIGUER and ROGERS 1981; WOOD 1980). HAMMOND (1965) found that even in domestic rabbits (when they are on a low plane of nutrition) summer anoestrus occurs.

It is hard to believe that this ancestral pattern would still exist in an animal that has been in our temperate coastal climate at least since 1250 A.D. (RENTENAAR 1978). Individuals are supposedly selected for maximum reproductive value. There is individual variation in littering frequency, that, if genetically determined, should enable natural selection to act.

There is evidence for the influence of density, and also for that of food quality on the breeding pattern. In this study summer anoestrus occurred only in 1978 and 1980, years with a high population density, but not in 1979 when population density was low (fig. 3, tab. 8). A similar influence of population density was also found by LLOYD (1970). The growth rates of the young found in this study were within the usual range. So, in spring and summer there seems to have been sufficient food of high quality. Young born at summertime had the same chances of survival as the others (table 12) hence the number of offspring from an individual would increase if that individual continued breeding as long as possible. However, the high survival rate of late-born young in 1979 might have been caused by the fact that they experienced less than usual food competition from the early-born young (GARDON 1986).

It is possible that longer breeding would lower the survival chance of the doe and hence her chance to reproduce in the following spring. This has not been measured in our study.

However, rabbits are known to be able to breed much longer than three months, even in our temperate climate (Brambell 1943).

Population density affects food quality. At a low population density (e. g. in 1979) rabbits have more choice of food plant and can enhance the quality of their diet.

Generally, the concentration of protein in grasses is lowest in June/July and increases again in August/September (McNeill and Southwood 1978). Also the species composition of the vegetation changes unfavourably after the end of April (table 9).

Recently Boyd (1986) described that the administration of 6-methoxybenzoxalinone (6-MBOA) to rabbits can prevent reproductive regression when the breeding season would normally end. A precursor of 6-MBOA is especially prevalent in the growing shoots of grasses. A regrowth of the vegetation often occurs in August/September.

So intrinsic responses of production size to population density do occur, but they might to a large extent be the results of the interaction between rabbit and vegetation.

Recruitment into the autumn population

After the decrease in population numbers in winter 1978–79, the longer breeding season could not compensate for the later start of breeding and smaller litter size that also resulted from the harsh weather conditions. Recruitment was not sufficient to allow recovery of the population from the extra mortality in that winter.

Interestingly, Cooke (1981) found in S. W. Australia that rabbit populations needed two years to recover from a drastic change in density and the same is mentioned by Sheail (1971).

The rate of increase of the population might have been slowed down by predation of foxes on nestlings and young (Tittensor 1981).

Conclusion

Although predation is important and may slow down the rate of increase in rabbit population numbers, the potential maximum density reached by the population was set by the quantity and quality of food. The availability of food varied stochastically with the weather. In some years, e. g. 1978–79, severe food shortage caused a major reduction in population numbers. In other years, e. g. 1979–80 and 1980–81, rabbit densities were not curtailed by food shortage. In this latter case, low rabbit numbers and abundant food may give the impression that rabbit numbers are kept below the limit set by the food supply by other factors. However no mechanisms would prevent the population from rising to its food limit again.

Acknowledgements

The first author is grateful to the PWN for cooperation and support. The students J. L. Mulder, Judith van Genderen, Els Nijssen, J. Damm, M. van Nierop, R. Akkermans, Els Jans, F. Distelbrink, H. van de Water, Sj. de Waard assisted in the collecting of data. J. M. J. Herzberg made the figures. N. Straw kindly corrected the english. We thank dr. S. Broekhuizen, Research Institute for Nature Management, Prof. dr. K. Bakker, and dr. E. v. d. Meijden, University of Leiden, for their interest during the study and the advice on the manuscript.

Zusammenfassung

Der Einfluß des Nahrungsangebot auf die Populationsdichte von Kaninchen, Oryctolagus cuniculus (L.), in einem niederländischen Dünengebiet

Die Populationsdichte von Kaninchen wurde in einem gemäßigten maritimen Klima hinsichtlich folgender Frage untersucht: Wird sie durch Selbstregulation kontrolliert, durch Feinddruck und Krankheit, oder steigt die Individuenzahl bis zu einer durch das Nahrungsangebot bedingten Höchstgrenze? Die Studie wurde an mehreren Beobachtungsstellen in einem Dünenreservat an der

Küste durchgeführt. Im Herbst und Winter wurden in einem Experiment zusätzliche Nahrung angeboten. Der strenge Winter 1978–79 führte bei vielen Kaninchen zum Hungertod, aber in den folgenden Jahren nahm die Populationsdichte wieder zu, erreichte jedoch nicht die durch das Nahrungsangebot ermöglichte Höchstgrenze.

Die Wurffrequenz pro Jahr war nicht hoch, wahrscheinlich beeinflußt durch die große Populationsdichte. Die Länge der Fortpflanzungssaison wurde bestimmt durch die Wechselwirkung zwischen Populationsdichte und Nahrungsqualität. Erwachsene Kaninchen wurden von Füchsen und Hermelinen erbeutet, manchmal auch von Katzen oder Iltissen. Feinddruck und andere Mechanismen, die möglicherweise für eine Regulation der Bestandsentwicklung verantwortlich sein könnten, waren nicht stark genug, um die Zahl der Kaninchen permanent unter der durch das Nahrungsangebot bedingten Grenze zu halten. Die Gründe dafür werden besprochen.

References

Andersson, M.; Dahlback, M.; Meurling, P. (1979): Biology of the wild rabbit, *Oryctolagus cuniculus,* in southern Sweden. 1. Breeding season. Viltrevy **11,** 103–127.

Bell, J. (1977): Breeding season and fertility of the wild rabbit, *Oryctolagus cuniculus* (L.) in North Canterbury, New Zealand. Proc. N. Zl. Ecol. Soc. **24,** 79–83.

Boyd, I. L. (1986): Effect of daylength on the breeding season in male rabbits. Mammal Rev. **16,** 125–130.

Brambell, F. W. (1943). The reproduction of the Wild Rabbit *Oryctolagus cuniculus* (L.). Proc. Zool. Soc. London **114,** 1–45.

Broekhizen, S.; Bouman, E.; Went, W. (1986). Variation in the timing of nursing in the Brown Hare *(Lepus europaeus)* and the European Rabbit *(Oryctolagus cuniculus).* Mammal Rev. **16,** 139–144.

Cooke, B. D. (1981): Food and dynamics of rabbit populations in inland Australia. In: Proc. First World Lagomorph Conf., Guelph, Ontario. 633–648. Ed. by K. Myers and C. D. MacInnes.

Cowan, D. P.; Garson, P. J. (1985): Variations in the social structure of rabbit populations: causes and demographic consequences. In: Behavioural Ecology. Ed. by R. M. Sibley and R. H. Smith. Oxford: Blackwell Scientific Publ., 537–555.

Daly, J. C. (1981): Effects of social organization and environmental diversity on determining the genetic structure of a population of the wild rabbit, *Oryctolagus cuniculus.* Evolution **35,** 689–706.

Delibes, M.; Hiraldo, F. (1981): The rabbit as prey in the Iberian mediterranean ecosystem. In: Proc. First World Lagomorph Conf., Guelph, Ontario. Ed. by K. Myers and C. D. MacInnes. 614–622.

Doing, H. (1964): Vegetatie. In: Recreatie en Natuurbescherming in het Noordhollands Duinreservaat. Suppl. 2. Meded. ITBON nr. **69c.** Belmontia II. Ecology fasc. 11.

Dudszinski, M. L.; Mykytowycz, R. (1960): Analysis of weights and growth rates of an experimental colony of wild rabbits. CSIRO Wildl. Res. **5,** 102–115.

Dunnet, G. M. (1956): Growth rate of young rabbits, *Oryctolagus cuniculus* (L.) CSIRO Wildl. Res. **1,** 66–67.

Dunsmore, J. D. (1971): Biology of the wild rabbit. IV. Austr. J. Zool. **19,** 355–370.

Erlinge, S. (1983): Demography and dynamics of a stoat *Mustela erminea* population in a diverse community of vertebrates. J. An. Ecol. **52,** 705–727.

Erlinge, S.; Goransson, G.; Hansson, L.; Hogstedt, G.; Liberg, O.; Nilsson, I. N.; Nilsson, T., von Schantz, T.; Sylven, M. (1983): Predation as a regulating factor on small rodent populations in southern Sweden. Oikos **40,** 36–52.

Errington, P. L. (1946): Predation and vertebrate populations. Quart. Rev. Biol. **21,** 144–177, 221–246.

Feen, P. J. van der (1963): Hoe en wanneer zijn wilde konijnen in Europa verspreid geraakt? Biol. Jaarb. Dodonea, Gent **31,** 237–243.

Fenner, F.; Ratcliffe, F. N. (1965): Myxomatosis. Cambridge: Cambridge Univ. Press.

Flux, J. E. C.; Fullagar, P. J. (1983): World distribution of the rabbit *(Oryctolagus cuniculus).* Acta Zool. Fenn. **174,** 75–79.

Garson, P. J. (1986): Intraspecific influences on juvenile recruitment rate in Rabbits. Mammal Rev. **16,** 195–196.

Gibb, J. A. (1977): Factors affecting population density in the wild rabbit *Oryctolagus cuniculus* (L.) and their relevance to small mammals. In: Evolutionary Ecology. Ed. by B. Stonehouse and Chr. Perrins. London Basingstoke: Macmillan Press. 33–46.

Gibb, J. A.; Ward, G. D.; Ward, C. P. (1969): An experiment in the control of a sparse population of wild rabbits *(Oryctolagus cuniculus)* in New Zealand. N. Zl. J. Sci. **12,** 509–534.

— — — (1978): Natural control of a population of rabbits, *Oryctolagus cuniculus* (L), for ten years in the Kourarau enclosure. N. Zl. Dept. of Sci. and Ind. Res., Wellington, Bulletin **223.**

Gillham, M. E. (1955): Ecology of the Pembrokeshire islands III. The effect of grazing on the vegetation. J. Ecol. **43**: 172–206.
Hammond, J. (1965): The effects of high and low planes of nutrition on the reproduction in rabbits. N. Zl. J. Agr. Res. **8,** 708–717.
Hewson, R.; Healing, T. D. (1971): The stoat, *Mustela erminea,* and its prey. J. Zool. **164,** 239–244.
Hughes, R. L.; Rowley, I. (1966): Breeding season of female wild rabbits in natural populations in the Riverina and Southern Tablelands districts of New South Wales. CSIRO Wildl. Res. **11,** 1–10.
King, C. M. (1977): Stoat Mustela erminea. In: Handbook of British Mammals: Ed. by G. B. Corbert and H. N. Southern. Oxford, London, Edinburgh, Melbourne: Blackwell Sci. Publ. 331–338.
Lack, D. (1954): The natural regulation of animal numbers. Oxford: Clarendon Press.
Lloyd, H. G. (1970): Variation and adaptation in reproductive performance. Symp. Zool. Soc. Lond. **26,** 165–188.
— (1980): The red fox. London: Batsford.
— (1981): Biological observations on post-myxomatosis wild rabbit populations in Britain 1955–1979. In: Proc. First World Lagomorph Conf., Guelph, Ontario. Ed by K. Myers and C. D. MacInnes. 623–628.
Lloyd, H. G.; Cowan, D. P. (1968): Some observations on the breeding burrows of the wild rabbit, *Oryctolagus cuniculus,* on the island of Skokholm. J. Zool., Lond. **156,** 540–549.
McIlwaine, C. P. (1962): Reproduction and body weights of the wild rabbit *Oryctolagus cuniculus* (L.) in Hawke's Bay, New Zealand. N. Zl. J. Sci. **5,** 325–341.
McNaughton, S. J. (1983): Compensatory growth as a response to herbivory. Oikos **40,** 329–336.
McNeill, S.; Southwood, T. R. E., (1978): The role of nitrogen in the development of insect/plant relationships. In: Biochemical aspects of plant and animal coevolution. Ed. by J. B. Harborne. Phytochem. Soc. Europ. Symp. Ser. no **15,** 77–98. London: Academic Press.
Minot, C. S.; Taylor, E., (1905): Normentafeln zur Entwicklungsgeschichte der Wirbeltiere. Jena: Gustav Fischer.
Mueller-Dombois, D.; Ellenberg, D. (1974): Aims and methods of vegetation ecology. New York: John Wiley.
Mulder, J. L. (1985a): Spatial organization, movements and dispersal in a dutch red fox *(Vulpes vulpes)* population: some preliminary results. Rev. Ecol (Terre et Vie) **40,** 133–138.
— (1985b): Invloed van de vos op wulpen en fazanten in het Noordhollands Duinreservaat. De Ned. Jager **90,** 564–566.
Myers, K. (1958): Further observations on the use of field enclosures for the study of the wild rabbit. CSIRO Wildl. Res. **3,** 40–49.
— (1964): Influence of density on fecundity, growth rates, and mortality in the wild rabbit. CSIRO Wildl. Res. **9,** 134–137.
— (1971): The rabbit in Australia. In: Dynamics of Populations. Ed. by P. J. den Boer and G. R. Gradwell. Wageningen Pudoc: 478–506.
Myers, K.; Poole, W. E., (1961): A study of the biology of the wild rabbit, *Oryctolagus cuniculus* (L.), in confined populations. II. The effect of season and population increase on behaviour. CSIRO Wildl. Res. **6,** 1–41.
— — (1963): A study of the biology of the wild rabbit, *Oryctolagus cuniculus* (L.), in confined populations. V. Population dynamics. CSIRO Wildl. Res. **8,** 16–203.
Myers, K.; Gilbert, N. (1968): Determination of age of wild rabbits in Australia. J. Wildl. Manage. **32,** 841–849.
Myers, K.; Schneider, E. C., (1964): Observations on reproduction, mortality and behaviour in a small, free-living population of wild rabbits. CSIRO Wild. Res. **9,** 138–143.
Mykytowycz, R.; Gambale, S., (1965): A study of the inter-warren activities and dispersal of wild rabbits, *Oryctolagus cuniculus,* living in a 45-ac. paddock. CSIRO Wildl. Res. **10,** 111–123.
Nicholson, A. J. (1954): An outline of the dynamics of animal populations. Austr. J. Zool. **2,** 9–65.
Niewold, F. J. J. (1976): De bestudering van de oecologie van de vos *(Vulpes vulpes)* in verband met zijn rol bij de verspreiding van rabies. 1–119, I-XXXV, Rijksinstituut voor Natuurbeheer, Arnhem.
Parer, I. (1977): The population ecology of the wild rabbit, *Oryctolagus cuniculus* (L.), in a Mediterranean-type climate in New South Wales. Austr. Wildl. Res. **4,** 171–205.
Parer, I.; Fullagar, P. J. (1986): Biology of rabbits, Oryctolagus cuniculus, in subtropical Queensland. Austr. Wildl. Res. **13,** 545–559.
Poole, W. E. (1960): Breeding of the wild rabbit, *Oryctolagus cuniculus* (L.), in relation to the environment. CSIRO Wildl. Res. **5,** 21–43.
Rentenaar, R. (1978): De vroegste geschiedenis van het konijn in Holland en Zeeland. Holland: reg. hist. tschr. **10,** 2–16.
Rogers, P. M. (1981): The wild rabbit in the Camargue, Southern France. In: Proc. First World Lagomorph Conf., Guelph, Ontario. Ed. by K. Myers and C. D. MacInnes. 587–599.
Schantz, T. von (1984): 'Non-breeders' in the red fox *Vulpes vulpes:* a case of resource surplus. Oikos **42,** 59–65.

SHEAIL, J. (1971): Rabbits and their history. Newton Abbot: David and Charles.
SINCLAIR, A. R. E. (1975): The resource limitation of trophic levels in tropical grassland ecosystems. J. An. Ecol. **44**, 497–520.
SKIRA, I. J. (1978): Reproduction of the Rabbit, *Oryctolagus cuniculus* (L.), on Macquarie Island, Subantarctic. Aust. Wildl. Res. **5**, 317–326.
SOLOMON, M. E. (1969): Population dynamics. London: Edward Arnold.
SORIGUER, R. C.; ROGERS, P. M. (1981): The European wild rabbit, *Oryctolagus cuniculus* (L.) in Mediterranean Spain. In: Proc. First World Lagomorph Conf., Guelph, Ontario. Ed. by K. Myers and C. D. MacInnes. 600–613.
SOUTHERN, H. N. (1940): The ecology and population dynamics of the wild rabbit *Oryctolagus cuniculus).* Ann. appl. biol. **27**, 509–526.
TITTENSOR, A. H. (1981): Rabbit population trends in southern England. In: Proc. First World Lagomorph Conf., Guelph, Ontario. Ed. by K. Myers and C. D. MacInnes. 629–632.
TYNDALE-BISCOE, C. H.; WILLIAMS, R. M. (1955): A study of natural mortality in a wild population of the rabbit. N. Zl. J. Sci. Techn. **36(B)**, 561–580.
WALLAGE-DREES, J. M. (1983): Effects of food on onset of breeding in rabbit, *Oryctolagus cuniculus* (L.), in a sand dune habitat. Acta Zool. Feen. **174**, 57–59.
— (1986): Seasonal changes in the condition of Rabbits, *Oryctolagus cuniculus* (L.), in a coastal sand dune habitat. Z. Säugetierkunde **51**, 26–36.
— (1988): A field study on seasonal changes in the circadian activity of rabbits. Z. Säugetierkunde (in press).
WALLAGE-DREES, J. M.; DEINUM, B. (1986): Quality of the diet selected by wild rabbits (*Oryctolagus cuniculus* [L.]) in autumn and winter. Neth. J. Zool. **36**, 438–448.
WATSON, A.; MOOS, R. (1970): Dominance, spacing behaviour and aggression in relation to population limitation in vertebrates. In: Animal populations in relation to their food resources. Ed. by A. Watson. Oxford and Edinburgh: Blackwell Sci. Publ. 167–220.
WHEELER, S. H.; KING, D. R. (1985): The European rabbit in south-western Australia. II. Reproduction. Austr. Wildl. Res. **12**, 197–212.
WOLFF, J. O. (1980): The role of habitat patchiness in population dynamics of snowshoe hares. Ecol. Monogr. **50**, 111–130.
WOOD, D. H. (1980): The demography of a rabbit population in an arid region of New South Wales, Australia. J. An. Ecol. **49**, 55–79.

Author's address: Dr. J. MARIJKE WALLAGE-DREES, Department of Population Biology, University of Leiden, P.O. Box 9516, NL-2300 RA Leiden, The Netherlands

Z. Säugetierkunde 54 (1989) 324–328

ISSN 0044-3468

Flank rubbing in genets (*Genetta genetta* L.): Histological correlates

By J. J. Roeder, C. Kelche and E. Vogel

Laboratoire de Psychophysiologie and Laboratoire de Neurobiologie des Comportements, Université Louis Pasteur, Strasbourg, France

Receipt of Ms. 15. 2. 1988

Abstract

Studied was the histological structure of skin sections of various body regions in genets *(Genetta genetta)*. Genets exhibit two main scent marking behaviours: anogenital marking which involves specialized glands (perineal) and flank rubbing which does not imply well delimited external glands. The aim of this study carried out on one adult female, was to determine whether enlarged cutaneous glands are present in the body regions involved in flank rubbing. Histological sections of various body regions were analyzed with an image analysis computer. Results indicate that increased density and size of sebaceous glands can be found in body regions involved in flank rubbing compared to other body regions. These results are related to previous behavioural data showing that certain olfaction related behaviours could have evolved to act as visual displays.

Introduction

Body rubbing is a widespread phenomenon in carnivores and can be divided into:

1. Scent rubbing: rubbing movements on odoriferous substances such as chemical substances, food or scent marks (e.g. in wolves, Peters 1974; Ryon et al. 1986);
2. Rubbing movements not oriented on scented substrates. Such behaviours have generally been described as comfort (Gangloff 1975) or as scent marking behaviours (e.g. in stoats, Erlinge 1982).

Several hypotheses concerning the significance and origin of such rubbing movements have been proposed (for review see Rieger 1979) but the functions of such behaviours remain poorly understood. In genets *(Genetta genetta)*, flank rubbing has generally been considered as a scent marking behaviour in the same way as ano-genital marking (Gangloff and Ropartz 1972; Roeder 1978). It consists of rubbing the cheek, neck and dorsal parts of the flank against unscented vertical substrates (Roeder 1980). But whereas ano-genital marking is associated with specialized localized glands (perineal glands), flank rubbing does not involve such well delimited skin glands. However, previous studies (Roeder 1980) have shown that both types of marking could convey olfactory information about individual identity and physiological status. The aim of the present study was to determine whether enlarged cutaneous glands are present in the body regions involved in flank rubbing and therefore whether this behaviour can be considered as a scent marking behaviour.

Methods

Skin samples (N=11 from right and left body parts of the animal) were collected from one dead adult female genet. These samples were taken from different body regions involved in flank rubbing (cheek, neck, anterior flank, median flank) or not involved (ventral flank, forelegs). After 8 days exposure to Bouin's picroformol fixative, tissue blocks were embedded in paraffin and cut into 7–10 micron thick sections. Sections tangent to the surface of the skin and providing from these samples were stained with haematoxylin and eosine. Samples were analyzed with an image analysis computer (Ibas 1, Zeiss)

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5405-0324 $ 02.50/0

coupled with a camera microscope system (magnification from microscope to graphic screen giving a value of 151 for 1 mm). The data were recorded for 40 histological sections from each body area.

The parameters recorded were: Density (number of sebaceous glands shown on the screen), areas (mean area of the sebaceous glands on each section), perimeter (mean perimeter of the sebaceous glands on each section), and D max. (mean distance between the two furthest points located on the perimeter of the sebaceous glands).

The number of acini for each section varied from 17 to 34. Results were analyzed with an analysis of variance considering 10 (for density) or 20 (for areas) samples chosen randomly for each body region.

Results

No specialized glands comparable to the perineal glands were found in the different skin sections. Skin sections show sebaceous glands which are found in association with hair follicles (Fig. 1). No structural differences were observed between the different body regions.



Fig. 1. Histological section of the skin from the medial flank (×75). 1 = muscle fibres, 2 = sebaceous glands, 3 = blood vessel, 4 = hair shaft, 5 = connective tissue

Results are shown in table 1. The highest density of sebaceous glands is found in the cheek area, although it does not differ significantly from those found in the two flank regions (anterior and median flank). The only statistically significant difference between body regions involved in flank rubbing, concerns cheek and neck areas (Table 2). The most striking result is that all body regions involved in flank rubbing have a significantly higher density compared to body areas which are not involved in flank rubbing.

The same result emerges for the mean areas of sebaceous glands in various body regions. No statistically significant differences appear between the two flank regions. The highest mean areas are found on the neck. This phenomenon can be explained by the lower sebaceous gland density in this region compared to the other body regions involved in flank rubbing. Perimeter values are correlated to the mean areas values. Dmax are indicated

Table 1. **Densities and sizes of sebaceous acini from various body parts**

Body regions	Density	Mean areas	Mean perimeters	D. max
Cheek	13.8 (1.8)	549.9 (61.1)	91.4 (6.7)	32.5 (2.5)
Flank anterior region	13.4 (2.6)	646.6 (81.9)	101.5 (11.5)	32.3 (5.9)
Flank medial region	12.8 (2.7)	657.7 (82.9)	100 (9.3)	32 (3.5)
Neck	11.4 (1.8)	861 (109.2)	111.9 (7.8)	37.4 (3)
Forelegs	9.6 (1.4)	507.4 (10.5)	91 (11.5)	–
Flank ventral region	9.3 (1.4)	394.6 (109.1)	81.5 (9.9)	32.8 (4.3)

( ) = S.D.

Table 2. **Statistical comparison on densities and mean areas of sebaceous glands from various body regions**

Body regions	Density F1/18	Density P	Area F1/38	Area P
Cheek/Forelegs	33.07	<.001	22.59	<.001
Cheek/Flank medial	.94	N.S	21.91	<.001
Cheek/Flank anterior	.16	N.S	17.69	<.001
Cheek/Flank ventral	36.67	<.001	30.82	<.001
Cheek/Neck	8.64	=.008	123.44	<.001
Flank anterior/Flank medial	.253	N.S	.20	N.S
Flank anterior/Neck	3.88	N.S	49.49	<.001
Flank anterior/Flank ventral	18.34	<.001	67.89	<.001
Flank anterior/Forelegs	16.08	=.001	18.5	<.001
Flank medial/Neck	1.84	N.S	43.89	<.001
Flank medial/Flank ventral	12.86	=.002	73.70	<.001
Flank medial/Forelegs	10.97	=.004	21.3	<.001
Neck/Flank ventral	7.86	=.011	182.4	<.001
Neck/Forelegs	5.97	=.023	12.13	=.001
Flank ventral/Forelegs	.21	N.S	21.4	<.001

in order to give a representation of the shapes of sebaceous glands. The only difference is found in the neck area where the acini seem to be more elongated than in other body regions.

Figure 2 gives a representation of density and size of the sebaceous glands on the genet's body.

Discussion

Although our data have to be verified, the present preliminary study shows a higher density of sebaceous glands in the body regions involved in flank rubbing. These histological results confirm previous behavioural data showing that such rubbing movements could convey olfactory information. According to JOHNSON's (1973) definition of scent marking ("Scent marking is a behaviour by which glandular secretions are deposited on the ground or onto objects in an animal's environment"), flank rubbing in genets can be considered as a true scent marking behaviour comparable to perineal marking.

Nevertheless, previous studies (ROEDER 1983) have demonstrated that:

1. Spontaneous flank rubbing appears very rarely in isolated animals (less than 0.1 episode per hour) compared to perineal marking (F = 0–50 per hour)

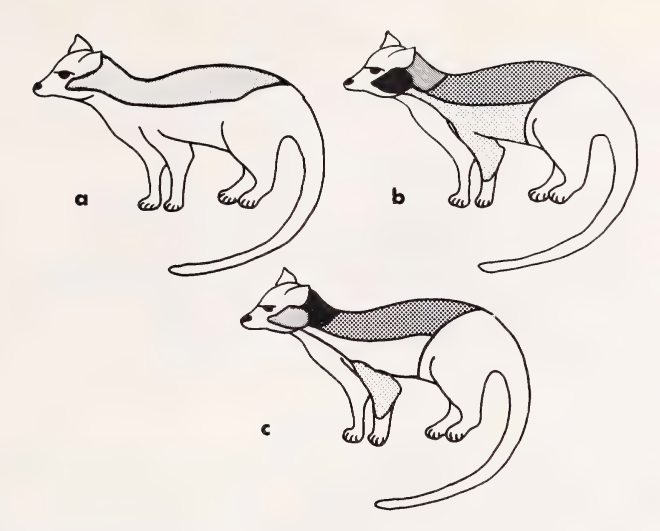


Fig. 2. Schematic representation of (a) body regions involved in flank rubbing, b: sebaceous glands densities in various body regions, c: sebaceous glands mean areas in various body regions; the darkest regions correspond to the highest density or area, the lightest regions to the lowest density or size

2. Flank rubbing frequencies increase markedly during agonistic encounters (2.4 to 3.2 episodes per hour), and
3. During agonistic encounters flank rubbing is generally associated (more than 60 % of all cases) with a visual signal: piloerection of the dorsal crest and the tail which acts as a threat signal. Conspecifics respond to this signal by exhibiting a piloerection even when they are only under visual contact with the emettor (pers. obs.).

Such olfactory related rubbing movements used as threat signals have been described in other carnivores. For example, in stoats *(Mustela erminea)*, body rubbing is used in close aggressive contacts between conspecifics and seems to be a threat signal (Erlinge et al. 1982). In the same way, in dwarf moongooses *(Helogale undulata rufula)*, cheek rubbing also acts as a threat signal: in the presence of an active or a passive threat, marking with the cheek glands increases in frequency and intensity (Rasa 1973). But neither of these authors indicate that such rubbing movements are associated with visual displays.

The present study suggests that some olfactory related behaviours have been ritualized during evolution and seem to function as visual displays. Although data dealing with this problem are scarce, it appears that some marking behaviours can be associated with visual signals (appeasement or threat) in carnivores (Rieger 1979) and primates (Schilling 1980). Phylogenetically, flank rubbing in genets could have evolved from a primary scent marking behaviour (deposition of skin gland secretions) to a visual signal (flank rubbing associated with piloerection) through a physiological response to the social environment. In fact the secretions of cutaneous glands reach the skin surface as a result of rubbing and contraction of the arrector muscles of hair (Flood 1986). Therefore, this scent marking behaviour could have been related to a visual display in order to increase skin gland production. It would be interesting to carry out comparative studies to improve understanding of such evolutionary phenomena.

It remains to complete the present data by extending this histological study to other female and male subjects. However it appears that to combine histological substrates and correlated behavioural events could bring out a new understanding of some behaviours whose function remains unexplained.

Acknowledgements

We are very grateful to Dr. J. ANDERSON for valuable discussion and for correcting the English and to Mr. C. ROEDER for translating the german summary.

Zusammenfassung

Flankenreiben bei Ginsterkatzen (Genetta genetta): Histologische Untersuchung

Es gibt zwei wesentliche Markierungsarten bei Ginsterkatzen *(Genetta genetta)*: Markierungen mittels perinealer Drüsen und Flankenreiben. Die vorliegende Arbeit beschreibt die Histologie von Talgdrüsen, die sich in Höhe der Flanken befinden und beweist, daß Dichte und Größe der Talgdrüsen in den entsprechenden Regionen bedeutsamer sind als in anderen Körperteilen. Die Ergebnisse werden auf Grund der zuvor beschriebenen Verhaltensweisen analysiert.

References

ERLINGE, S.; SANDELL, M.; BRINCK, C. (1982): Scent marking and its territorial significance in stoats, *Mustela erminea*. Anim. Behav. **6**, 53–61.

FLOOD, P. (1985): Sources of significant smells: The skin and other organs. In: Social odours in mammals 1. Ed. by R. E. Brown and D. W. MacDonald. Oxford: Clarendon Press. Vol. **1**, 19–36.

GANGLOFF, B. (1975): Beitrag zur Ethologie der Schleichkatzen (Bänderlinsang), *Prionodon linsang* (Hardw.) und Bänderpalmenroller, *Hemigalus derbyanus* (Gray). Zool. Garten, **45**, 329–376.

GANGLOFF, B.; ROPARTZ, P. (1972). Le répertoire comportemental de la genette, *Genetta genetta* (Linné). La Terre et la Vie **4**, 489–560.

JOHNSON, R. P. (1973): Scent marking in mammals. Anim. Behav. **21**, 521–535.

PETERS, R. P. (1974): Wolf sign: scents and space in a wide-ranging predator. Ph.D. thesis, University of Michigan, Ann Arbor, MI.

RASA, A. O. E. (1973): Marking behaviour and its social significance in the African dwarf mongoose, *Helogale undulata rufula*. Z. Tierpsychol. **32**, 293–318.

RIEGER, I. (1979): Scent rubbing in carnivores. Carnivore **2**, 17–25.

ROEDER, J. J. (1978): Marking behaviour in genets (*Genetta genetta* L.): Seasonal variations and relation to social status in males. Behaviour **67**, 149–156.

— (1980): Marking behaviour and olfactory recognition in genets (*Genetta genetta* L., Carnivora: Viverridae). Behaviour **72**, 200–210.

— (1983): Etude des interactions sociales entre mâle et femelle chez la genette (*Genetta genetta* L.): relations entre marquage olfactif et agression. Z. Tierpsychol. **61**, 293–310.

RYON, J.; FENTRESS, J. C.; HARRINGTON, F. H.; BRAGDON, S. (1986): Scent rubbing in wolves *(Canis lupus)*: The effect of novelty. Can. J. Zool. **64**, 573–577.

SCHILLING, A. (1980): Bases morphologiques et comportementales de la communication olfactive chez les Prosimiens. Doctorat d'état es Sciences Naturelles, Université de Paris VI.

Authors' address: Dr. J. J. ROEDER, Mrs. E. VOGEL, Laboratoire de Psychophysiologie and Dr. C. KELCHE, Laboratoire de Neurobiologie des Comportements, 7 rue de l'Université, F-67000 Strasbourg, France

Z. Säugetierkunde 54 (1989) 329–330

ISSN 0044-3468

WISSENSCHAFTLICHE KURZMITTEILUNGEN

The type locality of *Cynictis penicillata coombsii* Roberts, 1929 and *Gerbillus paeba coombsii* Roberts, 1929

By P. J. Taylor and J. A. J. Meester

Department of Biology, University of Natal, Durban

Receipt of Ms. 27. 12. 1988

Roberts (1929) described two taxa, *Cynictis penicillata coombsii* (p. 90–91; synonym of *C. p. penicillata* – Meester et al. 1986) and *Gerbillus paeba coombsii* (p. 98–100; currently *Gerbillurus paeba coombsi* – Meester et al. 1986) from the farm Swarthoek (22° 59′ S; 29° 53′ E), in the Zoutpansberg District, northern Transvaal, South Africa. Both holotypes were collected in 1927 by Mr. Cecil Coombs, and catalogued in the Transvaal Museum by Austin Roberts (*C. p. coombsi*: TM 4877, old male, coll. 18th April, 1927; *G. p. coombsi*: TM 4898, old male, coll. 19th June, 1927). The name Swarthoek (or Zwarthoek, in the older spelling) appears on the specimen labels, accession register and catalogue cards, as well as in subsequent publications by Roberts (1951) and later workers (Ellerman et al. 1953; Meester et al. 1986). In his description of *G. p. coombsi*, Roberts (1929:99) refers to this locality as being "west of the Sand River and a little north of the [Zoutpansberg] mountain range".

On a recent visit to the area by one of us (P.J.T.) it was established in conversation with an elderly farmer, Mr. Vivian Fourie, of Farm Dorpsrivier, Waterpoort, that Mr. Coombs had owned the farm Swarthaak, on the flats just north of the Zoutpansberg Mountain Range and west of the Sand River (22° 52′ S; 29° 28′ E). Swarthoek, on the other hand, lies east of the Sand River, on the southern slopes of the Zoutpansberg Mountains, just north of Louis Trichardt, some 60 km south of Swarthaak.

Both *C. penicillata* and *G. paeba* are almost exclusively confined to the South West Arid zone (Davis 1962), occurring on a sandy substrate throughout their range. Swarthoek, on the southern slopes of the Zoutpansberg, would therefore be a most atypical habitat for both species. On the other hand, the area north of the Zoutpansberg, in which Swarthaak is located, is characterised by the occurrence of a relic blook of Kalahari sands, and the associated fauna is more typical of the Kalahari Desert in Botswana than of the northern Transvaal Savanna, including both *C. penicillata* and *G. paeba*, as well as the Gemsbok, *Oryx gazella*.

Considering the fact that Mr. Coombs owned the farm Swarthaak, and not Swarthoek, that Swarthaak offers a suitable habitat for both species while Swarthoek does not, and that Swarthaak (but not Swarthoek) lies west of the Sand River and north of the Zoutpansberg, the conclusion is inescapable that Roberts for some reason recorded the wrong farm name as type locality for these two taxa. Accordingly we designate Swarthaak, and not Swarthoek, as type locality for both *C. p. coombsi* and *G. p. coombsi*.

References

Davis, D. H. S. (1962): Distribution patterns of Southern African Muridae, with notes on some of their fossil antecedents. Ann. Cape Prov. Mus. **2**, 56–76.

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5405-0329 $ 02.50/0

Ellerman, J. R.; Morrisson-Scott, T. C. S.; Hayman, R. W. (1953): Southern African mammals 1758–1953: a reclassification. Trustees, British Museum (Natural History), London.

Meester, J. A. J.; Rautenbach, I. L.; Dippenaar, N. J.; Baker, C. M. (1986): Classification of Southern African mammals. Transv. Mus. Monograph No. **5**, 1–359.

Roberts, A. (1929): New forms of African mammals. Ann. Transv. Mus. **13**, 82–121.

— (1951): The Mammals of South Africa. Johannesburg: "The mammals of South Africa" Book Fund.

Authors' address: Peter Taylor and J. Meester, Department of Biology, University of Natal, King George V Ave., Durban 4001, RSA

Z. Säugetierkunde 54 (1989) 331–333

ISSN 0044-3468

Intraspecific variation in facing-water behaviour of *Spalacopus cyanus* (Octodontidae, Rodentia)[1]

By. D. Reise and M. H. Gallardo

Instituto de Ecologia y Evolución, Universidad Austral de Chile

Receipt of Ms. 13. 01. 1989

Individuals of the fossorial, gregarious and monotypic genus *Spalacopus* Wagler, 1832 from the arid north in Chile were more hesitant to swim than individuals from the rainy southern distributional range. This differential behaviour is likely to affect intraspecific genetic and phenotypic variation especially in such a narrow longitudinal distribution along the western slope of the Andes. The latitudinal distribution extends over 1000 km (30° S to 38° S), sectioned by more than 10 large transversal fluvial systems (Fig. 1). It has been suggested that low levels of genetic and phenotypic variability in *Spalacopus* are caused by cohesive gene flow promoted by its alleged high vagility (Reig 1970; Reig et al. 1972). However, this hypothesis does not consider the discontinuous geomorphology of Chile and besides, it conflicts with a preliminary analysis of morphological variation in *Spalacopus* (Reise 1976). In this context, the facing-water behaviour and swimming ability poses interesting questions to the hypothesized high vagility, distributional pattern, and genetic structure of this species.

Spalacopus cyanus (Molina, 1782), the "cururo", lives in various habitats like coastal dunes, dry steppes, prairies, desertic stream beds and cultivated areas from sea-level up to 3400 m above M.S.L. in the Andes. Rainfall averages within its distributional range from scattered showers in the desert to heavy rainfalls in the south.

Nine cururos were caught in northern Chile (Huentelauquén 31° 37′ S – 71° 31′ W and Los Vilos 31° 55′ S – 71° 00′ W) during July and August 1987. Just before sampling this northern region was subjected to unusually heavy rainfalls which flooded wide areas. It was not possible to observe where the animals stayed during inundation. After water level descended the animals reappeared in their burrows. In northern cultivated valleys an analogous situation takes place every springtime when fields are flooded for irrigation. Four additional animals were caught in the isolated and southernmost population of *Spalacopus* (Quirihue 36° 15′ S – 72° 31′ W), in May before the 1987 rainy season.

The cururos' swimming ability was tested in an aquarium (65×45×15 cm) filled with 10 cm water at 25 °C. One animal at the time was placed on a 6×6 cm central stone elavated 1 cm above water level. The facing-water behaviour and swimming ability were observed and the time the animals spend on the stone was recorded. All specimens were taken out of the water after swimming for 1 min. Each animal was subjected to the experiment only once to avoid experience. The observer moved 2 m away from the aquarium and stood motionless while the experiment was taking place.

For gregarious cururos this exposure constituted an extreme situation as they normally disappear down their burrows when any disturbance is perceived. This experimental design stressed the animals and at the same time, forced them to contact water.

It took more than 5 min to four specimens (2 ♀, 2 ♂) from Los Vilos (coastal dunes in northern Chile) to voluntarily slide into the water. The animals repeatedly touched water with their vibrissae and mouth and circled round with tripling steps. One male and one

[1] Partially funded by DID UACH RS85-17, S-88-06 and DAAD.

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5405-0331 $ 02.50/0

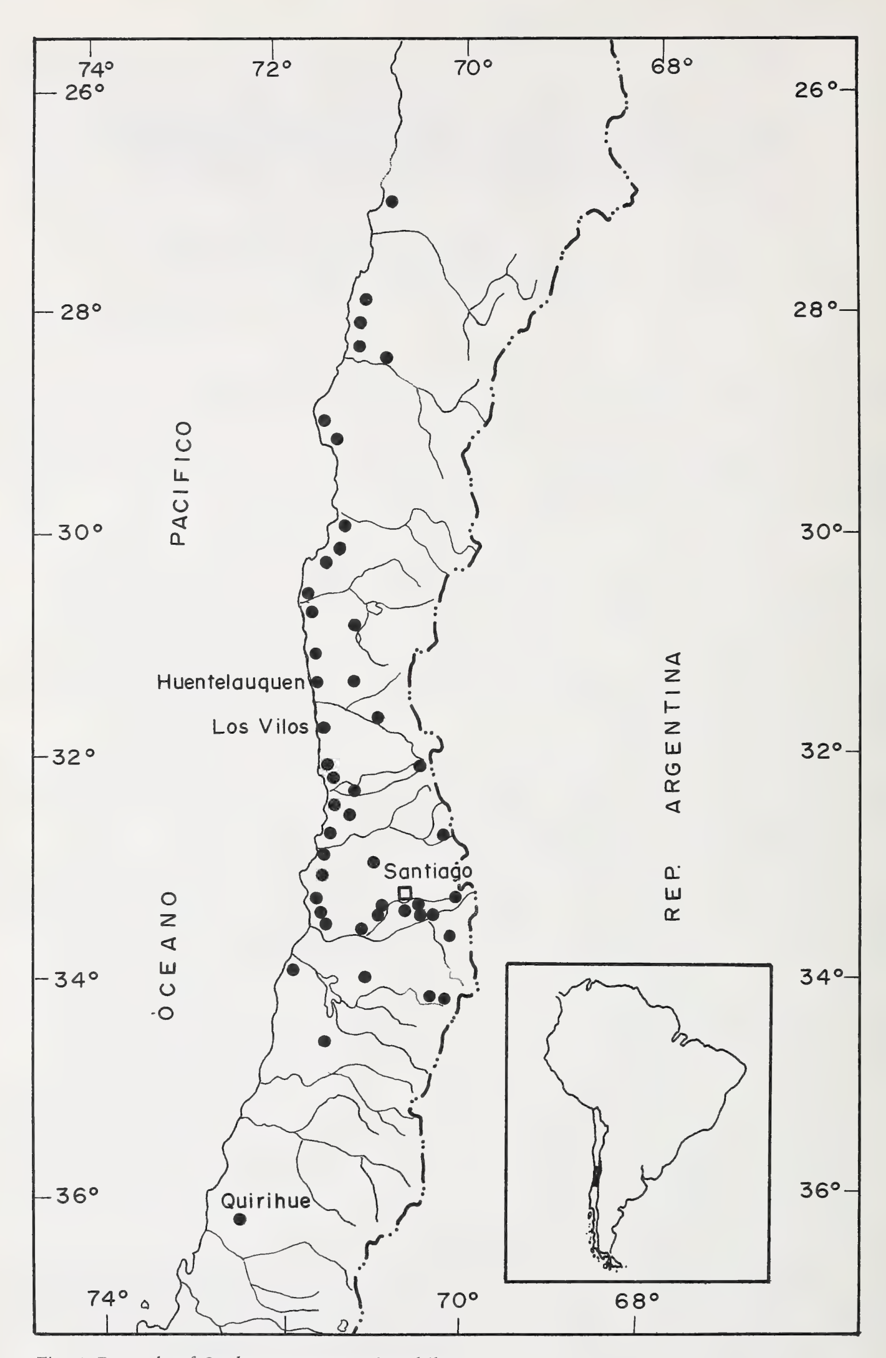


Fig. 1. Records of *Spalacopus cyanus*, in Chile

female emitted their typical warning call for several seconds while still on the stone. After 20 min on the stone, one male jumped up in direction of the nearest wall of the aquarium and started to swim.

Four out of five (3 ♀, 2 ♂) specimens from Huentelauquén (dry steppe with flooded areas) waited around 1 min to voluntarily come into water. Apparantly males required more time than the females (3; 5 min ♂, 1; 2 min ♀). All animals tried water repeatedly. One male emitted the warning call before swimming. A juvenile female animal entered water as soon as she was placed on the central surface.

Southern cururos (2 ♀, 2 ♂) from Quirihue (extensively cultivated mediterranean shrubsteppe) faced water without trying and hesitation. They did not emit their warning calls but started to swim immediately.

All specimens tested had no difficulties in swimmning for 1 min. They swam with strong movements of fore- and hindlegs as described by Hickman (1988). Heads were lifted higher than noted by him. The back had an slightly opisthotonic posture, noses, eyes and ears were always above water. After the test, wet animals wallowed by themselves in dry sawdust and pushed themselves among the bodies of the remaining members of their social group searching for close contact.

The facing-water behaviour differed considerably between the northern and southern population samples tested. Water seemed to be a strange element for northern cururos, as they entered only after hesitation and presumed compulsory stress. Apparently, specimens from the southern population had no difficulties in facing water. This behaviour is probably an indication of familiarity with this element due to frequent rainfalls in their natural habitat.

The poor swimming ability (projected distance 38 m) recorded by Hickman (1988) and our observed rejection to water might be a decisive factor for longitudinal migration too and concomitantly hampers the distribution, at least of the major northern populations of *Spalacopus*. The assumed high migration rates (Reig 1970; Reig et al. 1972) may only occur in restricted areas not dissected by rivers and should not be the basis of general statements concerning the degree of genetic and phenotypic variability in this species.

The small and peripheral population from Quirihue described by Osgood (1943) as *Spalacopus cyanus maulinus* is geographically isolated from the main species distribution. Taking into account the above mentioned geomorphical features of the country the observed familiarity with water probably accounts for its dispersion pattern and actual distant separation from the main distributional area of the species.

Literature

Hickman, G. C. (1988): The swimming ability of *Ctenomys fulvus* (Ctenomyidae) and *Spalacopus cyanus* (Octodontidae), with reference to swimming in other subterranean mammals. Z. Säugetierkunde **53**, 11–21.

Osgood, W. H. (1943): The Mammals of Chile. Field Mus. Nat. Hist. Zool. Ser. **30**, 1–268.

Reig, O. A. (1970): Ecological notes on the fossorial octodont rodent *Spalacopus cyanus* (Molina). J. Mammalogy **51**, 592–601.

Reig, O. A.; Spotorno, A.; Fernandez, R. (1972): A preliminary survey of chromosomes in populations of the Chilean burrowing octodont rodent *Spalacopus cyanus* Molina (Caviomopha, Octodontidae). Biol. J. Linn. Soc. **4**, 29–38.

Reise, D. (1976): Taxonomische Untersuchungen an der unterirdisch lebenden, chilenischen Trugratte *Spalacopus cyanus* (Molina, 1782) (Caviomorpha, Octodontidae). Vortrag, 50. Hauptvers. Dt. Ges. Säugetierkunde, Kurzfassung.

Authors' address: Dr. Detlef Reise and Dr. Milton H. Gallardo, Instituto de Ecologia y Evolución, Universidad Austral de Chile, Casilla 567, Valdivia, Chile

BUCHBESPRECHUNGEN

Grzimek, B. (Hrsg.): **Grzimeks Enzyklopädie Säugetiere – Band 1.** München: Kindler Verlag 1988. 648 Seiten, zahlreiche Abb., Lexikon-Großformat. Leinenausgabe: DM 148,–, ISBN 3-463-42001-5; Luxusausgabe (Halbleder): DM 198,–, ISBN 3-463-42001-5

Band 1 dieser Enzyklopädie erschien aus redaktionellen Gründen nach den Bänden 2 und 4, über die bereits Besprechungen in dieser Zeitschrift veröffentlicht wurden (Bd. 2 in 53/6, Bd 4 in 53/4).

Dieser erste Band enthält nach einem einleitenden Abschnitt zur Kenntnis der gesamten Klasse (mit Kapiteln u. a. über die Stammesgeschichte, den Körperbau und die Körperfunktionen, über ökologische Zusammenhänge, das Verhalten und Fragen des Artenschutzes) im systematischen Teil (etwa Zweidrittel des Gesamtumfanges) Beiträge über Monotremata, Marsupialia, Insectivora, Macroscelidea, Chiroptera und Dermoptera. In der schon gewohnten Weise werden jeder Ordnung zwei einleitende Seiten mit „Basisinformationen" vorangestellt, die eine rasche Information u. a. über das System, auffällige Merkmale und Grundzüge der Biologie ermöglichen. Die Textteile bringen nach einer Einleitung jeweils Informationen zur Stammesgeschichte und im wesentlichen dann die Darstellung der rezenten Vertreter der jeweiligen Gruppe. Je nach dem Umfang der behandelten Gruppe verfahren die Autoren bei der Anordnung des Stoffes unterschiedlich; zumeist erfolgt eine Gliederung nach systematischen Gesichtspunkten, bei den Chiropteren bot sich eine solche nach biologischen an. Übersichtliche Tabellen – zumeist auf dem Familienniveau – bringen zu einzelnen, repräsentativen Arten Angaben über körperliche Merkmale und zur Biologie (Fortpflanzung, Lebensablauf, Nahrung, Lebensweise etc.). Eine große Anzahl von Photographien ausgezeichneter Qualität und bis zur Größe einer Doppelseite sowie zahlreiche Zeichnungen, diese besonders in dem einleitenden Abschnitt, erleichtern das Verständnis der Textinhalte; viele der Photos vermitteln darüber hinaus ganz einfach auch, wie faszinierend die dargestellten Tiere sind.

Die Arbeit des Abfassens der 41 Kapitel dieses Bandes haben sich 20 Autoren geteilt, die als ausgewiesene Kenner für ihr Fach bzw. ihre Gruppe den Stoff in vergleichbar komprimierter aber immer gut verständlicher Form und vor allem auf dem aktuellen Wissensstand dargestellt haben. Eine besondere Bedeutung kommt naturgemäß dem einleitenden Abschnitt dieses Bandes zu. Wenn man auch hinsichtlich der Auswahl einiger Details dieses Stoffes andersartig gewichten könnte, und der Fachmann diese oder jene Information hinterfragen möchte, so vermittelt dieser Teil doch in abgerundeter Form die wichtigen Grundlagen für das Verständnis der ganzen Klasse; Informationsvielfalt und gute Lesbarkeit sind hier sicher nicht immer leicht miteinander zu vereinbaren gewesen. In dem systematischen Teil dieses Bandes beanspruchen naturgemäß Marsupialia, Insectivoren und Chiropteren die größte Aufmerksamkeit. Eine gewisse Uneinheitlichkeit in der Präsentation des Stoffes zeigt sich darin, daß die Beuteltiere – im wesentlichen wohl durch die Zahl der Autoren bedingt, die z. T. sogar innerhalb der einzelnen Familien wechseln – eine vergleichsweise breite Darstellung erfahren (mit fast dem doppelten Umfang der jeweils beiden anderen gewichtigen Gruppen). Hierbei werden die einzelnen Familien, nicht so sehr unter dem Aspekt des Inhaltlichen als vielmehr der formalen Gestaltung, sehr viel stärker hervorgehoben als in den übrigen Gruppen. Dies mag mit der Materie nicht so vertraute Leser verwirren. Trotz dieser kritischen Anmerkungen gelingt auch diesem Teil des ersten Bandes in eindrucksvoller Weise die Vermittlung eines vertieften Wissens über die Formenmannigfaltigkeit der behandelten Ordnungen und über die Vielfalt der Anpassungen ihrer Mitglieder.

Ohne Zweifel können auch Fachleute diesen Band mit Gewinn lesen oder als Nachschlagewerk benutzen. Aber seine Bedeutung und die der Serie reicht darüber hinaus. In Zeiten zunehmender Naturentfremdung ist es hoch zu schätzen, daß sich Autoren und Verlag zusammengefunden und in vermutlich nicht wiederholbarer Form ein Werk geschaffen haben, das mit seinen kompetenten Texten und den hervorragenden, aufwendigen Illustrationen sicher auch ein breiteres Publikum ansprechen wird.

H. Schliemann, Hamburg

Zupanc, G. K. H. (Hrsg.): **Praktische Verhaltensbiologie.** Parey's Studientexte 61. Berlin, Hamburg: Parey 1988. 274 S., 109 Abb., 17 Tab., DM 39,80. ISBN 3-489-62936-1

This book comprises a series of chapters written by experienced scientists and teachers on their particular behavioural speciality and animal species. As such, each section represents years of accumulated experience on the behaviour of the species concerned and the species' application in student practicals. The authors have selected out of the entire behavioural repertoire of their animals those aspects of behaviour that can be reliably replicated in the laboratory. This reliability marks the success or failure of any behaviour practical.

The book presents a wide variety of laboratory experiments that can either be used as demonstrations or as practical exercises for students ranging from school to University level. The experiments

suggested vary from simple constructs requiring little apparatus and knowledge of theoretical issues in ethology to more extensive (and expensive) ones which presuppose a theoretical etho-physiological or ethological background and the presence of specialised laboratory equipment. The animals suggested for use to illustrate different aspects of behavioural theory range from protozoa on the one hand, through insects and fish to birds and mammals on the other. An important inclusion is the chapter on optimal holding conditions for experimental animals, since physical and mental well-being has a profound influence on behavioural performance. Apart from general advice on holding conditions, each chapter contains a section giving more detailed information on the species concerned which will be of great value to instructors unfamiliar with them.

The book contains a subtle blending of theory and practice. Each experimental section includes suggested topics for seminars and a list of pertinent literature, as well as suggested themes for future research. This makes it especially valuable at the University level where specific topics can be discussed in detail.

Although the book is designed for use in German-speaking countries, due to its excellent treatment of the subject, its application could be far more widespread. One useful addition from this point of view would be the suggestion of alternative species for use in different countries. This may not be a problem with commercially available animals but becomes one when species endemic to the European continent are concerned. In general, the book can be considered, in the world literature, as being one of the most advanced and complete presentations of its kind and should find a wide application at both School and University level. O. Anne E. Rasa, Pretoria

Altmann, D.: **Harnen und Koten bei Säugetieren.** Neue Brehm-Bücherei 404. Wittenberg-Lutherstadt: Ziemsen 1988. 162 S., 33 Abb., 7 Tab. DM 20,–. ISBN 3-7403-0162-7

This handbook provides a comprehensive coverage of the present knowledge on micturation and defaecation in mammals. The subject is approached from a descriptive standpoint and body postures during elimination illustrated for several species. The behaviour pre- and post-elimination is also described in detail. Much of the data originates from studies in zoos, which could have a practical application for the improved holding of captive animals. The use of faeces and urine in various social contexts is discussed succinctly and a large section of the book consists of tables listing the presence or absence of a variety of behaviour patterns associated with elimination in a wide variety of mammals. The author concludes the survey with a species list incorporating the known information on eliminative behaviour for each of the species mentioned.

This is a useful handbook for anyone requiring information on mammalian eliminative behaviour and the importance of elimination products in the species social life. It allows easy comparisons between species and the literature is fairly comprehensive. My one criticism is the paucity of the English literature included, since this would have increased the number of species which could have been mentioned in the species lists, thus enhancing this study especially from the comparative point of view. In general, this handbook will be of value as a reference work to a wide audience ranging from behavioural scientists on the one hand to zoo-keepers and anyone who deals with captive mammals on the other. O. Anne E. Rasa, Pretoria

Wijnstekers, W.: **The evolution of CITES.** A reference to the Convention on International Trade in Endagered Species of Wild Fauna and Flora. Lausanne: Secretariat of CITES 1988. 270 pp. P. O. Box 78, CH-1000 Lausanne. Swiss Francs 30,–

If one has to write honestly about the history of international nature conservation, it will be a story of small successes and great disappointments. The explosive growth of the human population, the rapid loss of biotopes, the incorrect exploitation of natural resources, plain greed and ignorance are the elements which caused and which are causing the disappearance of so many species of animals and plants. This is well illustrated by the actual situation concerning rhinos and elephants. The moment of their extinction is nearing rapidly.

One of the very few successes in international nature conservation is the Washington Convention, the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). This convention, iniated by IUCN, took effect on 1-VII-1975 and at present most civilized nations are parties to it. Although the loss of habitats is the most important danger, the trade in wild animals and plants and their products is a very significant factor causing the disappearance of species. Just one example may suffice – in the years 1984 and 1985 alone, the countries of the European Community imported and exported 17,904 wild-caught non-human primates for laboratories, zoos, etc. This concerns only the EC, and to that number must be added the animals sent to the USA and Japan, not

to mention the smaller consumer countries like Sweden and Israel. Without the regulations of CITES this number would have been several times larger and many representatives of endangered species would have been among them.

It is strange, if not embarrassing, that so few university-trained biologists are interested in the Washington Convention, let alone are actively engaged in it. An important reason may be that there is so little up-to-date literature on the subject. The well-written popular introduction by Tim Inskipp and Sue Wells (1979) "International Trade in Wildlife" (Earthscan-London) is now somewhat dated. A new edition translated into several languages would be most useful. All the other publications are hard to find; government reports, articles in specialized journals, etc.

It is therefore a pleasure to announce that a highly technical book on the Washington Convention has been published recently. It is not easy to read; the history of the convention, the rules and regulations, the changes and amendments are subjects quite different from what biologists normally study. But if one is seriously interested in practical nature conservation, one has to take notice of this book. For persons preparing courses on nature conservation, for people working with conservation organisations, for civil servants dealing with international conventions and their national implementation, the book is a must.

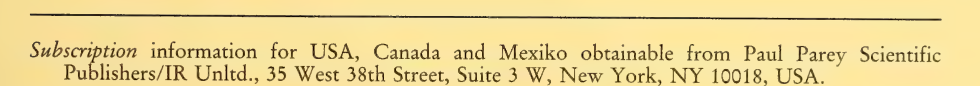
Now the world is getting more accessible each day and more crowded, we cannot work exclusively on academic subjects, but we have to take care of international nature conservation too. If it only would be for our self-preservation. P. J. H. van Bree, Amsterdam

Tinker, S. W.: **Whales of the world.** Honolulu: Bess Press 1988; 310 pp., numerous unnumbered illustr. Distributed by E. J. Brill, Leiden, New York, København, Köln. US $ 22,–. ISBN 90-04-08954-3

It is quite clear that cetaceans are now very popular. Numerous books on whales and dolphins have been published during the last decade. They range from simple booklets to coffee table books and serious publications. The books are written by cetologists with much personal experience, by clever compilers and by voluminous writers treating every subject they encounter. It is therefore very difficult to buy a book on Cetacea relying only on the title.

The book discussed here is a well written compilation with all the good and bad aspects of such a publication. It treats the origin and evolution of whales, the anatomy of living whales (taxonomy, synonymy, the species, their biology, distribution, etc) and it closes with a selected bibliography, an appendix on measurements and an index. The book is abundantly illustrated with drawings and photographs (many of which do not show to full advantage due to the paper on which they have been printed).

The publication is a good popular introduction to cetology. Especially handy for students and for teachers at secondary schools. The author is fond of long vernacular names, like the White-headed or Gray Grampus, the North Pacific Giant Four-toothed Whale and Soberby's North Sea Beaked Whale. It is evident from the treatment of the genera *Stenella* and *Orcaella* that the typescript was finished some years before the actual publication. Sometimes one comes across odd mistakes, like the occurrence of *Orcaella brevirostris* along the East African coast, but in general the number of mistakes is limited. P. J. H. van Bree, Amsterdam



Subscription information for USA, Canada and Mexiko obtainable from Paul Parey Scientific Publishers/IR Unltd., 35 West 38th Street, Suite 3 W, New York, NY 10018, USA.

Erscheinungsweise und Bezugspreis 1989: 6 Hefte bilden einen Band. Jahresabonnement Inland: 318,– DM zuzüglich 13,80 DM Versandkosten, Gesamtpreis 331,80 DM einschließlich 7 % Mehrwertsteuer. Jahresabonnement Ausland: 318,– DM zuzüglich 18,– DM Versandkosten. Das Abonnement wird zum Jahresanfang berechnet und zur Zahlung fällig. Es verlängert sich stillschweigend, wenn nicht spätestens am 15. November eine Abbestellung im Verlag vorliegt. Die Zeitschrift kann bei jeder Buchhandlung oder bei der Verlagsbuchhandlung Paul Parey, Spitalerstraße 12, D-2000 Hamburg 1, bestellt werden. Die Mitglieder der „Deutschen Gesellschaft für Säugetierkunde" erhalten die Zeitschrift unberechnet im Rahmen des Mitgliedsbeitrages.

Z. Säugetierkunde 54 (1989) 5, 265–336

Vol. 54 (6), 337–408, Dezember 1989 ISSN 0044-3468 C 21274 F

ZEITSCHRIFT FÜR SÄUGETIERKUNDE

INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde





Verlag Paul Parey Hamburg und Berlin

This journal is covered by Biosciences Information Service of Biological Abstracts, and by Current Contents (Series Agriculture, Biology, and Environmental Sciences) of Institute for Scientific Information

---

Die Zeitschrift für Säugetierkunde veröffentlicht Originalarbeiten und wissenschaftliche Kurzmitteilungen aus dem Gesamtgebiet der Säugetierkunde, Besprechungen der wichtigsten internationalen Literatur sowie die Bekanntmachungen der Deutschen Gesellschaft für Säugetierkunde. Verantwortlicher Schriftleiter im Sinne des Hamburgischen Pressegesetzes ist Prof. Dr. Harald Schliemann.

Zusätzlich erscheint einmal im Jahr ein Heft mit den Abstracts der Vorträge, die auf der jeweiligen Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde gehalten werden. Sie werden als Supplement dem betreffenden Jahrgang der Zeitschrift zugeordnet. Verantwortlich für ihren Inhalt sind ausschließlich die Autoren der Abstracts.

Manuskripte: Manuskriptsendungen sind zu richten an die Schriftleitung, z. Hd. Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Biologie-Zentrum, Neue Universität, Olshausenstr. 40–60, D-2300 Kiel. Für die Publikation vorgesehene Manuskripte sollen gemäß den „Redaktionellen Richtlinien" abgefaßt werden. In ihnen finden sich weitere Hinweise zur Annahme von Manuskripten, Bedingungen für die Veröffentlichung und die Drucklegung, ferner Richtlinien für die Abfassung eines Abstracts und eine Korrekturzeichentabelle. Die Richtlinien sind auf Anfrage bei der Schriftleitung und dem Verlag erhältlich.

Sonderdrucke: Anstelle einer Unkostenvergütung erhalten die Verfasser von Originalbeiträgen und Wissenschaftlichen Kurzmitteilungen 50 unberechnete Sonderdrucke. Mehrbedarf steht gegen Berechnung zur Verfügung, jedoch muß die Bestellung spätestens mit der Rücksendung der Korrekturfahnen erfolgen.

Fortsetzung 3. Umschlagseite

Z. Säugetierkunde 54 (1989) 337–346

ISSN 0044-3468

Artstatus der Alpenwaldmaus, *Apodemus alpicola* Heinrich, 1952

Von G. Storch und O. Lütt

Eingang des Ms. 10. 4. 1989

Abstract

Species status of Apodemus alpicola Heinrich, 1952

Apodemus alpicola Heinrich, 1952, originally described as a high-altitude subspecies of *A. flavicollis,* represents a morphologically well defined species. In the northern Alps (Kleinwalsertal and Montafon, Vorarlberg, Austria), *A. alpicola, A. sylvaticus,* and *A. flavicollis* occur syntopically. Obviously, *A. alpicola* is restricted to northwestern parts of the Alps. Diagnostic of *alpicola* is a complex of functionally unrelated features, i.e. coloration, skull proportions, body proportions, and molar cusp morphology. The conspicuous tail length, the elongate facial skull region, and the reduced cusp t9 on M2/ are autapomorphic features in which *alpicola* looks more specialized than *sylvaticus* and *flavicollis.*

Einleitung

In Mitteleuropa kommen nach bisheriger Kenntnis drei Waldmausarten der Untergattung *Sylvaemus* vor: *Apodemus (S.) sylvaticus* (Linnaeus, 1758) – Waldmaus, *A. (S.) flavicollis* (Melchior, 1834) – Gelbhalsmaus und *A. (S.) microps* Kratochvíl und Rosicky, 1952 – Zwergwaldmaus. Die westliche Verbreitungsgrenze von *microps* verläuft etwa entlang der Linie Breslau, Olmütz und Znaim in Mähren, Stockerau und Steinfeld in Niederösterreich und dem Neusiedlerseegebiet (Steiner 1978, Abb. 71). Die beiden anderen Arten besitzen in Zentraleuropa ein ausgedehntes gemeinsames Areal, das auch den Alpenraum einschließt (Niethammer 1978a, Abb. 68; 1978b, Abb. 69).

Die Zwergwaldmaus ist schon äußerlich an der grauen Färbung, den kurzen Hinterfüßen und Ohren und den kleinen Augen leicht zu erkennen, und sie unterscheidet sich auch durch kleinere Schädelmaße (z. B. der oberen Molarenreihe und den Foramina incisiva) von *sylvaticus* und *flavicollis.* Wald- und Gelbhalsmaus sind einander in Größe und Aussehen sehr ähnlich. In ihrem gemeinsamen Areal finden sich zudem intraspezifische Merkmalsänderungen, die klinal von Nord nach Süd konvergieren. Das führt dazu, daß sich die beiden Arten in den südlichsten Gebieten in Färbung und Größe sehr stark annähern können und nicht alle Individuen zuzuordnen sind. Eine verschiedentlich unterstellte zwischenartliche Bastardierung ist jedoch für das gesamte sympatrische Areal unbewiesen (Niethammer 1969). Am Monte Gargano, Italien, sind beide Arten kaum mehr nach der Kehlzeichnung und gar nicht nach der Größe unterscheidbar, es bestehen jedoch die gleichen Proteinunterschiede wie bei Tieren aus Deutschland (Gemmeke und Niethammer 1981). Hier ist also tatsächlich nachgewiesen, daß Wald- und Gelbhalsmaus auch dort gute Arten sind, wo morphologisch keine zuverlässige Unterscheidung mehr möglich ist.

In den nördlicheren Gebieten sind die Tiere in der Regel sicher zu bestimmen, soweit nicht typologisch an einem Einzelmerkmal festgehalten wird, sondern diagnostische Merkmalskombinationen herangezogen werden. Lediglich Populationen aus den Nordalpen scheinen nicht recht in dieses Bild zu passen. Die Trennung von Wald- und Gelbhalsmäusen gelang an Material aus Vorarlberg – im Gegensatz etwa zu ostösterreichischem – nicht oder nur ganz unbefriedigend (Bauer et al. 1967). Bei der Gelbhalsmaus scheinen in Europa Stufen in der geographischen Merkmalsprogression zu fehlen, oder sie ließen sich

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5406-0337 $ 02.50/0

zumindest bislang nicht nachweisen (Niethammer 1978a). Als Ausnahme sind nur Populationen der Unterart *A. f. alpicola* Heinrich, 1952 in den Nordalpen deutlich aus dieser klinalen innerartlichen Variation herausgehoben. *A. f. alpicola* unterscheidet sich in auffälliger Weise in den Proportionen des Gesichtsschädels von den angrenzenden Populationen der Nominatrasse *A. f. flavicollis* und gleichermaßen auch von *A. sylvaticus* (Reinwaldt 1955). Die Bauchfärbung von *A. f. alpicola* ist – ähnlich wie bei *A. sylvaticus* – grauweiß meliert und nicht leuchtend-weiß wie bei *A. f. flavicollis.* Allein diese Beobachtungen fordern zu einer Überprüfung des taxonomischen Ranges von *alpicola* auf.

Hinzu kommt aber noch das angenommene Verbreitungsmuster der beiden Gelbhalsmaus-Unterarten *alpicola* und *flavicollis.* Danach kommen beide sympatrisch vor und schließen einander nur in vertikaler Richtung aus. *A. f. alpicola* soll oberhalb, *A. f. flavicollis* unterhalb der 1000-m-Grenze leben (Heinrich 1951). Ein derartiger Sachverhalt scheint von vornherein ausgeschlossen. Es müßten sich nicht nur die Präferenzbiotope beider Unterarten extrem unterscheiden, sie müßten sogar in ökologisch und räumlich geschiedenen Lebensräumen beheimatet sein, um unvermischt bestehen zu können. Hierzu bietet aber weder die Vegetation noch die Geomorphologie der Nordalpen genügende Voraussetzungen. Auch ist zu erwarten, daß gerade bei der in Mitteleuropa stenöken Gelbhalsmaus eine ökologische Trennung von Unterarten nur höchst unscharf sein kann.

Es gilt daher die Alternative zu überprüfen, ob *alpicola* nicht eine eigene Art repräsentiert, d. h. ob in den Nordalpen nicht nur zwei sondern drei Waldmausarten vorkommen. Um an Sammlungsmaterial reproduktive Artschranken nachzuweisen, sollte nicht nur sympatrisches sondern syntopisches Vorkommen bei guter morphologischer Trennbarkeit der betreffenden Taxa belegt werden. Unter diesen Gesichtspunkten wurden unsere Sammelorte ausgewählt. Bei der Auswertung des Materials wurden nach Möglichkeit solche Merkmale herangezogen, die nicht miteinander funktionell korreliert sind (Färbung, Schädelproportionen, Molarenmorphologie, Größe) und somit als Merkmalskomplexe artdiagnostisch sein dürften.

Bisherige Angaben über *alpicola*

Heinrich (1951) beschrieb *A. f. alpinus* anhand von Material von der Typuslokalität Osterachtal (1100 m) im Allgäu sowie aus dem Berchtesgadener Land und der Steiermark. Später (Heinrich 1952) ersetzte er *alpinus* (präokkupiert durch *Mus sylvaticus alpinus* Burg, 1921) durch *alpicola.* Als wesentliche Unterart-Merkmale stellte er die auffallende Schwanzlänge, die dunkelgrau melierte Bauchfärbung und die verwaschene, häufig zu einem Längsstrich ausgezogene Kehlzeichnung heraus. Er bezog *alpicola* trotz der abweichenden Färbung aufgrund der großen Hinterfuß- und Schädellängen auf die Gelbhalsmaus und führte den deutschen Namen „Alpenwaldmaus“ ein.

Reinwaldt (1955) verglich Schädel der Typenserie mit solchen von *A. f. flavicollis* und *A. sylvaticus* aus Deutschland und Schweden. Er fand in der relativ größeren Diastema-Länge von *alpicola* einen deutlichen größenunabhängigen Formunterschied.

Bauer et al. (1967) stellten bei der Mehrzahl von Gelbhalsmäusen aus dem Montafon/Vorarlberg die Merkmale von *alpicola* fest, in anderen Vorarlberger Proben konstatierten sie unterschiedliche Merkmalskombinationen.

Von Lehmann und Knecht (1970) konnten in Liechtenstein in 1500 m Höhe die Alpenwaldmaus und in sich anschließenden tieferen Lagen typische Gelbhals- und Waldmäuse nachweisen. Unterseits „nicht ganz so weiß“ wie typische *A. f. flavicollis* gefärbte Tiere aus 1400 m wurden als Übergangsformen der beiden Vertikalrassen *alpicola* und *flavicollis* gedeutet.

Von Lehmann (1973) fand weitgehende Übereinstimmung von Ostschweizer Tieren aus Höhenlagen über 1000 m (Unterengadin, Münstertal) mit *alpicola*-Paratypen aus dem Osterachtal. Er unterschied sie wegen ihrer etwas helleren Bauchfärbung und etwas geringeren Schwanzlänge als *A. f. alpinus* Burg, 1921 von *alpicola.* Eine kleine Probe aus dem Bergell teilte er in *A. f. flavicollis* (Sammelorte in 700–900 m) und *A. f. alpinus* (aus 1000–1200 m) auf. *Mus sylvaticus alpinus* Burg, 1921 ist u. E. ein nomen nudum und nicht verfügbar.

Niethammer (1978a) wies deutlich auf die Sonderstellung von *A. f. alpicola* im Kontext der Unterartgliederung der Gelbhalsmaus in Europa hin.

Ergebnisse

Syntopisches Vorkommen von Alpenwaldmaus, Gelbhalsmaus und Waldmaus

Die Sammelorte wurden so ausgewählt, daß ihre geographische Lage zwischen Terra typica im Osterachtal und späteren Fundpunkten von *alpicola* (Liechtenstein, Vorarlberg, Ostschweiz) vermittelt und ihre Höhenlage keines der fraglichen Taxa Alpenwaldmaus, Gelbhalsmaus und Waldmaus ausschließen sollte. Es handelt sich einmal um das Kleine Walsertal (Vorarlberg, Österreich), wo entlang der Breitach in 1120–1160 m NN auf einer Strecke von etwa 2,5 km sowie am Bärguntbach um 1290 m NN auf etwa 1 km Länge gesammelt wurde, und zum anderen um Silbertal/Montafon (Vorarlberg, Österreich), wo die Sammelpunkte entlang der Litz in 890–990 m NN über eine Strecke von 1,5 km verteilt waren. Lebensraum war jeweils Wald mit steilen Hanglagen, der teilweise dichten feuchten Unterwuchs aufwies und von Lichtungen und Wiesen unterbrochen war.

Ziel der Feldarbeit war der Nachweis aller drei Taxa unmittelbar nebeneinander, was sowohl im Walsertal wie auch in Silbertal gelang. Sie leben somit sympatrisch und – entscheidend zur Bestätigung des Artstatus von *alpicola* – erwartungsgemäß auch syntopisch! Die drei Arten konnten auf wenigen Quadratmetern nebeneinander gesammelt werden. Unterschiedliche ökologische Präferenzen drückten sich nur insoweit aus als *sylvaticus* offenere Bereiche und Waldrand, *flavicollis* aber unterwuchsarmen Hochwald bevorzugte; *alpicola* war vorherrschend an lichteren Stellen mit reichlich niederer Pflanzendeckung, die eher feucht waren und oft ein starkes Bodenrelief aufwiesen. Die Sammeltermine waren so verteilt, daß syntopisches Vorkommen auch während der sommerlichen Reproduktionsphasen belegt ist.

Auswahl des Untersuchungsmaterials

In der Auswertung wurden die Materialproben von beiden Lokalitäten zunächst gesondert behandelt. Es sollte damit vermieden werden, daß geographische oder lokale Merkmalsänderungen die Trennbarkeit beeinflussen. Wie sich zeigte, können in der Darstellung der Ergebnisse beide Proben jedoch zusammengefaßt werden. Von beiden Fundorten liegen insgesamt 117 Tiere der Altersklassen 2–6 (nach Steiner 1968) vor (Senckenberg-Museum Frankfurt, SMF 59803-5, 59807-8, 59947-53, 61308-18, 61320-34, 61336, 61338-43, 61345-50, 68670-87, 68689-90, 68695, 68698-701, 68717, 70788-98, 70800, 70803-8, 73379-90, 73393-400, 73402-3). Davon wurden 48 als *alpicola* (Silbertal 34/Walsertal 14), 23 als *flavicollis* (8/15) und 46 als *sylvaticus* (6/40) bestimmt. Es ist nicht Ziel dieser Arbeit, das Verbreitungsgebiet von *alpicola* anhand von verfügbaren Sammlungsunterlagen zu kartieren. Als zusätzliche Belege wurden lediglich 6 Paratypen aus dem Osterachtal (Museum Alexander Koenig, Bonn, ZFMK 49.20-49.25; vgl. Hutterer 1984) aufgenommen.

Die Altersgrenze des berücksichtigten Materials wurde bewußt sehr tief angesetzt. Ausgeschlossen sind nur juvenile Exemplare der Altersklassen 1 bis „fast 2“, die teilweise noch im Jugendkleid sind. Aufsammlungen enthalten gewöhnlich einen großen Anteil heranwachsender Tiere, und sie können sich saisonal bedingt fast ausschließlich aus solchen zusammensetzen. Nach Möglichkeit sollten auch dafür Trennmöglichkeiten anhand von früh ausgeprägten oder altersunabhängigen Merkmalen gefunden werden.

Artunterschiede

Fellfärbung

Es bestätigt sich das von Heinrich (1951) dargestellte Bild. *A. alpicola* besitzt eine grauweiße (= dunkelgrau melierte) Unterseite, die bei 13 Exemplaren hellbräunlich ange-

flogen ist. Die gelbliche Kehlzeichnung ist immer längsgestreckt, und ihr Umriß ist gewöhnlich verwaschen. In 80 % der Tiere ist sie auf Hals und Brust beschränkt, bei den übrigen führt der Längsstrich bis auf den Bauch. 5 Tiere zeigen ein mehr oder weniger geschlossenes Halsband, das sich aber anders als bei *flavicollis* in einen Längsstrich fortsetzt.

A. sylvaticus hat ganz ähnlich *alpicola* eine grauweiße Ventralseite, die bei 4 Exemplaren braungelb überflogen ist. Die Kehlzeichnung ist gewöhnlich schwächer ausgeprägt als bei *alpicola*: Sie fehlt in 10 % der Tiere völlig, in 50 % ist ein Kehlfleck angedeutet, und in je 20 % ist ein schwacher bzw. betonterer Längsstrich über die Brustmitte vorhanden.

Die Unterseite von *A. flavicollis* ist weiß, bei einigen Tieren mit einem grauen Unterton. Die scharf umgrenzte Kehlzeichnung bildet in 80 % der Exemplare ein durchgehendes Halsband, bei den übrigen ist das Halsband beiderseits – in einem Fall sehr breit – unterbrochen.

Typisch gefärbte *A. alpicola* sind im Gelände gut zu erkennen. Bei abgeschwächter Kehlzeichnung können sie *sylvaticus*-ähnlich wirken. Sie können dann aber anhand ihrer langen Schwänze und Hinterfüße (s. u.) identifiziert werden.

Körpermaße

A. alpicola ist sehr langschwänzig. Die absoluten und relativen Werte der Schwanzlänge erreichen höhere Maxima und Mittel als bei *flavicollis* (Schwanzlänge von *alpicola* Maximum = 142 % und Mittel = 122 % der Kopfrumpflänge, bei *flavicollis* Maximum = 130 %, Mittel = 112 %). *A. sylvaticus* ist kürzerschwänzig als beide (Tab. 1–2).

Ein Vergleich der stark altersabhängigen Kopfrumpflängen ist im Hinblick auf die Altersstruktur der Materialproben kaum sinnvoll. Stichproben erwachsener Tiere (Tab. 2) deuten an, daß Alpenwaldmaus und Gelbhalsmaus etwa gleiche Körpergröße erreichen und die Waldmaus ein wenig kleiner bleibt.

Aussagekräftiger ist die Hinterfußlänge. Sie erreicht zu einem frühen Lebensalter das Endmaß und setzt daher keine so strikte Altersaufgliederung und die damit verbundene Reduzierung des Materials voraus. Alpenwaldmaus und Gelbhalsmaus haben lange Hinterfüße, ihre Maße variieren ungefähr in den gleichen Grenzen (Tab. 1–2). Die Waldmauspopulationen des Untersuchungsgebiets besitzen relativ große Hinterfußlängen, so daß ein Überschneidungsbereich mit *alpicola* und *flavicollis* um 24 mm herum besteht. Im Gelände fällt *alpicola* als sehr langschwänzig auf, und die großen Hinterfüße unterscheiden die Art meistens von *sylvaticus.*

Schädelmaße

Die Schädel von Alpenwaldmaus und Gelbhalsmaus erreichen ausgewachsen etwa die gleiche Länge, Waldmausschädel bleiben kleiner (Tab. 1–2). Das Condylobasalmaß drückt diese Gesamtlängen aus, kaschiert aber zwangsläufig Proportionsunterschiede.

A. alpicola unterscheidet sich sowohl von *flavicollis* als auch von *sylvaticus* durch Formunterschiede, die nicht allometrisch bedingt sind und somit als Artkriterien dienen. Der Gesichtsschädel von *alpicola* ist in auffälliger Weise gestreckt (Abb. 1–3) und der Hirnschädel dementsprechend relativ kürzer als bei den beiden anderen Arten (vgl. Reinwaldt 1955). Das Diastemamaß als Ausdruck der Facialschädellänge erreicht schon bei jugendlichen Alpenwaldmäusen die Werte adulter Gelbhalsmäuse, die wesentlich größere Condylobasallängen besitzen. Die *alpicola*-Proben zeigen also weit höhere Maximal- und Mittelwerte der Diastemalänge als die *flavicollis*-Proben (Abb. 4), obwohl Endmaß und offensichtlich auch Wachstum der Schädellängen übereinstimmen. *A. sylvaticus* schließt sich in den Proportionen des Gesichtsschädels *flavicollis* an (Abb. 1–3, Tab. 1–2). Die absoluten Diastemamaße sind deutlich kleiner als bei *alpicola,* wenn übereinstimmende Altersgruppen miteinander verglichen werden. Aber selbst in den altersmäßig nicht

Tabelle 1. **Körper-, Schädel- und Zahnmaße syntopischer *Apodemus*-Arten aus Silbertal (S) und Kleinwalsertal (W), Vorarlberg, Österreich. Die Streubereiche schließen Tiere der Altersklassen 2–6 ein**

Maß	n/	*flavicollis*	n/	*alpicola*	n/	*sylvaticus*	Fundort
Kr	8/	82–101	34/	81–108	6/	80–97	S
	15/	90–116	14/	84–96	40/	77–104	W
Schw	8/	100–117	33/	99–127	6/	83–99	S
	14/	97–122	13/	103–131	36/	80–104	W
Hf	8/	24.5–25.5	34/	23.5–26.0	6/	23.0–24.0	S
	15/	24.0–26.0	14/	24.0–26.5	40/	21.0–24.5	W
Cbl	8/	23.3–26.1	29/	22.8–26.5	6/	21.8–23.1	S
	11/	23.4–26.2	12/	23.6–25.1	34/	21.0–24.4	W
oZr	8/	4.2–4.50	34/	3.70–4.15	6/	3.6–3.8	S
	14/	4.0–4.45	13/	3.85–4.20	39/	3.4–3.8	W
Dia	8/	6.85–7.45	33/	7.0–8.5	6/	6.25–6.55	S
	15/	6.55–7.75	14/	7.0–8.2	40/	5.85–7.10	W
Fori	8/	4.95–5.50	33/	4.80–6.15	6/	5.05–5.40	S
	15/	4.75–5.55	14/	5.20–6.25	40/	4.75–5.90	W
ID	8/	1.24–1.50	33/	1.16–1.50	6/	1.12–1.26	S
	15/	1.24–1.56	14/	1.20–1.40	39/	1.08–1.36	W
M1/L	8/	2.12–2.32	34/	1.80–2.04	6/	1.76–1.88	S
B		1.32–1.40		1.20–1.40		1.12–1.20	
L	14/	1.96–2.12	14/	1.88–2.16	40/	1.68–2.00	W
B		1.28–1.40		1.20–1.40		1.12–1.28	
M2/L	8/	1.40–1.52	34/	1.20–1.40	6/	1.16–1.28	S
B		1.28–1.36		1.12–1.32		1.08–1.16	
L	14/	1.28–1.48	14/	1.28–1.40	40/	1.12–1.28	W
B		1.20–1.32		1.12–1.40		1.08–1.24	
M3/L	8/	0.98–1.00	34/	0.80–1.04	6/	0.72–0.84	S
B		0.96–1.06		0.84–1.00		0.76–0.88	
L	14/	0.88–1.08	14/	0.88–1.00	40/	0.56–0.88	W
B		0.88–1.00		0.88–1.04		0.68–0.92	

KR = Kopfrumpflänge, Schw = Schwanzlänge, Hf = Hinterfußlänge, Cbl = Condylobasallänge, oZr = obere Zahnreihenlänge, Dia = Diastemalänge, Fori = Länge der Foramina incisiva, ID = Incisivendicke, M1/ ... = erster ... oberer Molar, L = Länge, B = Breite

gegliederten Materialproben mit einem hohen Anteil heranwachsender Tiere überschneiden sich die Diastemalängen von *sylvaticus* und *alpicola* nur geringfügig (Abb. 4).

Die Länge der oberen Molarenreihe erreicht früh im Individualleben ihren Endwert und eignet sich daher ganz besonders zur Bestimmung. Die Zahnreihenlängen (Meßstrecke nach Niethammer 1969, Abb. 1) der syntopischen Populationen ordnen sich in der Reihenfolge *sylvaticus* < *alpicola* < *flavicollis* an. Die Mittelwerte der Proben sind durch gleiche Abstände voneinander getrennt (Mittelwert für *sylvaticus* = 3,63, *alpicola* = 3,93 und *flavicollis* = 4,25 mm), und die Überschneidungen der absoluten Maße von *alpicola* mit *sylvaticus* im unteren und mit *flavicollis* im oberen Streubereich sind nicht sehr bedeutend (Abb. 4, Tab. 1–2). Der oberen Zahnreihenlänge von *alpicola* kommt gegenüber *flavicollis* taxonomischer Eigenwert zu, denn sie repräsentiert – auf die Condylobasallänge bezogen – einen größenunabhängigen Proportionsunterschied.

Die Dicke der oberen Incisiven (Meßstrecke s. Abb. 5) verhält sich bei den drei Arten grundsätzlich wie die Zahnreihenlänge, nur ist sie stärker altersabhängig. Im Streudiagramm (Abb. 4) ist die Summe von oberer Zahnreihenlänge und Incisivendicke der Diastemalänge gegenübergestellt (die drei Arten waren zunächste nach anderen Merkmalen

Tabelle 2. **Einzelmaße von Stichproben adulter Tiere aus dem Material der Tab. 1. – Ak = Altersklasse (nach Steiner 1968)**

	Ak	Sex	Kr	Schw	Hf	Cbl	oZr	Dia	Fori	ID	M1/L	B	M2/L	B	M3/L	B	Fundort
alpicola																	
ZFMK 49.22	4–5	m	98	120	24.0	26.4	3.80	8.45	6.20	1.34	1.80	1.28	1.24	1.24	0.92	1.00	O.
ZFMK 49.25	3–4	m	100	120	25.0	25.9	3.90	8.40	5.90	1.32	1.69	1.28	1.28	1.24	0.84	0.92	O.
SMF 68 674	5	w	105	120	25.0	25.2	3.85	8.15	5.05	1.40	1.84	1.28	1.24	1.20	0.96	0.96	S.
SMF 68 683	5	w	97	115	24.0	25.0	3.95	7.90	5.00	1.42	1.80	1.28	1.20	1.28	1.00	0.96	S.
SMF 73 388	5	m	98	124	25.0	25.5	3.95	8.30	5.85	1.40	1.92	1.24	1.24	1.20	0.92	0.88	S.
SMF 73 389	5	w	95	127	25.0	25.3	3.90	8.25	5.00	1.34	1.88	1.28	1.28	1.28	0.96	1.00	S.
SMF 73 400	5	w	99	123	25.0	25.4	3.75	8.10	5.95	1.36	1.80	1.20	1.24	1.16	0.88	0.96	S.
flavicollis																	
SMF 73 393	5	w	90	101	25.0	25.1	4.45	7.15	5.00	1.48	2.28	1.40	1.40	1.36	1.00	1.06	S.
SMF 61 328	4	m	97	117	25.5	25.7	4.10	7.50	5.55	1.42	2.00	1.36	1.40	1.28	1.00	0.96	W.
SMF 61 339	4	m	106	115	26.0	25.1	4.30	6.95	5.15	1.32	2.08	1.32	1.44	1.24	0.92	1.00	W.
SMF 70 798	4–5	w	109	117	26.0	26.2	4.45	7.30	5.45	1.52	2.12	1.36	1.48	1.32	1.08	1.00	W.
SMF 70 800	5	w	97	122	25.0	25.3	4.10	7.10	5.15	1.56	2.00	1.28	1.32	1.24	1.00	0.88	W.
sylvaticus																	
SMF 68 682	4	w	97	99	24.0	23.1	3.65	6.55	5.10	1.26	1.76	1.16	1.24	1.12	0.80	0.80	S.
SMF 59 952	4	m	93	96	22.5	23.0	3.55	6.60	5.50	1.20	1.76	1.20	1.20	1.12	0.72	0.72	W.
SMF 61 308	4–5	w	100	100	24.5	24.2	3.60	7.10	5.50	1.36	1.80	1.16	1.20	1.12	0.64	0.68	W.
SMF 61 341	5	m	94	98	24.5	23.2	3.55	6.60	5.45	1.28	1.68	1.20	1.16	1.12	0.72	0.68	W.
SMF 61 342	4	m	94	101	23.5	23.6	3.75	6.85	5.85	1.24	1.92	1.24	1.16	1.20	0.88	0.76	W.

ZFMK = Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, SMF = Senckenberg-Museum, Frankfurt, O = Osterachtal im Allgäu, BRD (Paratypen); die übrigen Abkürzungen wie Tab. 1.

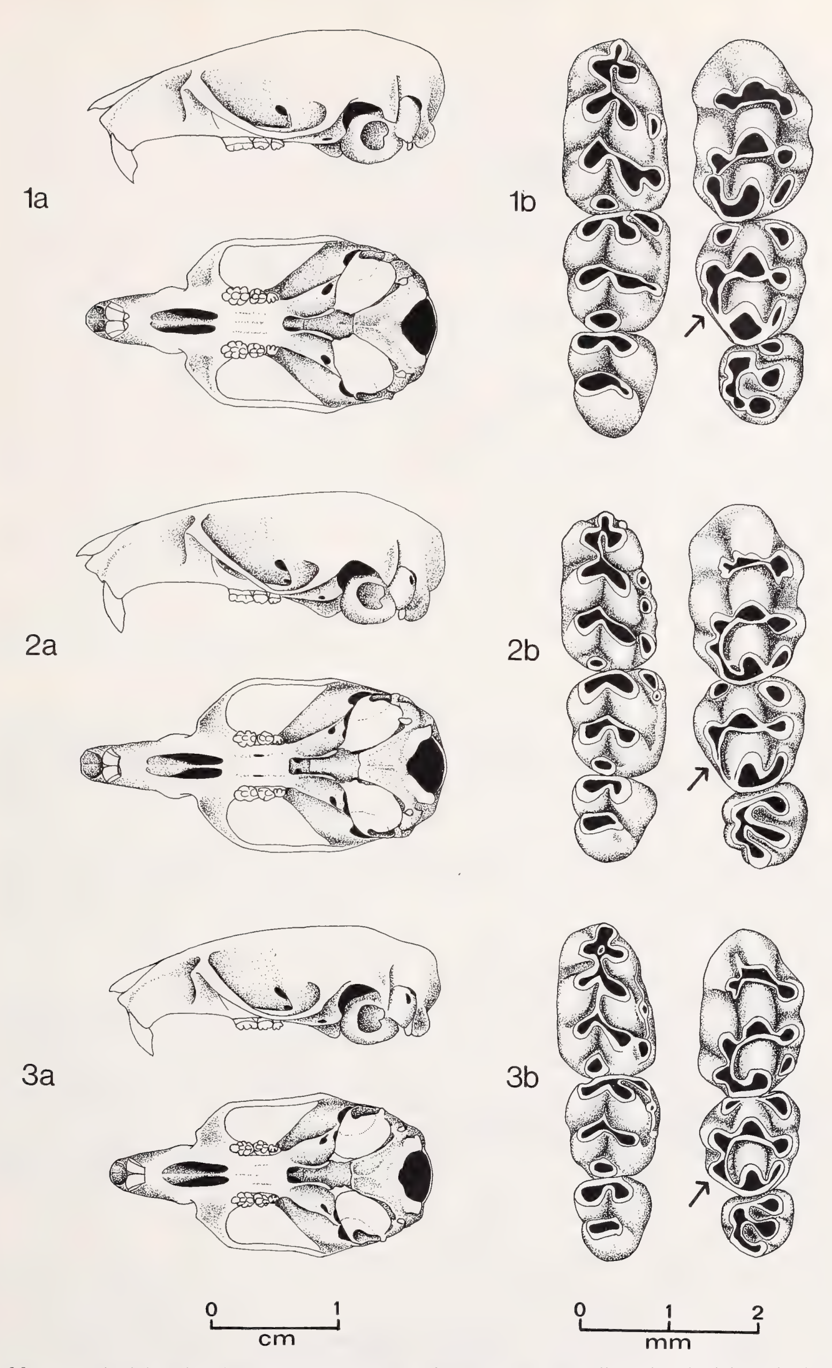


Abb. 1–3. Schädel und Gebisse syntopischer *Apodemus*-Arten aus Silbertal (Schädel) und Kleinwalsertal (Gebisse), Vorarlberg, Österreich. Schädel in Ansicht von lateral (oben) und ventral (unten). Untere (links) und obere (rechts) Molarenreihe in Ansicht von occlusal; die Pfeile markieren die Position des t9

Abb. 1. Apodemus flavicollis (a = SMF 73 393, b = SMF 70 794)

Abb. 2. Apodemus alpicola (a = SMF 73 388, b = SMF 70 807)

Abb. 3. Apodemus sylvaticus (a = SMF 68 682, b = SMF 59 949)

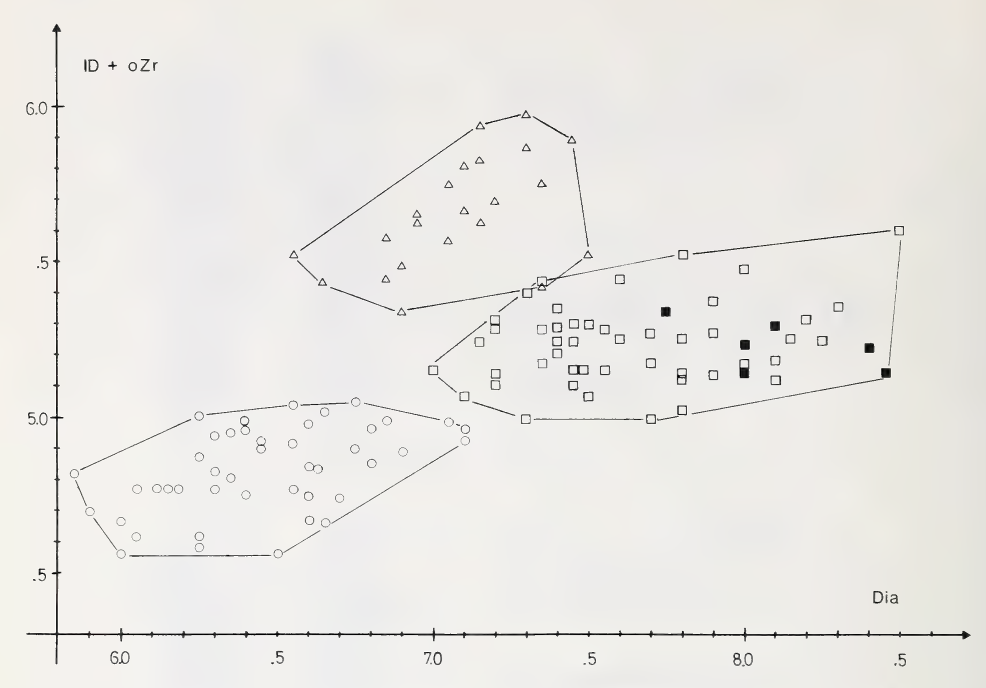


Abb. 4. Streudiagramm für die Diastemalänge und die Summe von oberer Zahnreihenlänge und Incisivendicke bei syntopischen Populationen von *Apodemus sylvaticus* (Kreise), *A. alpicola* (Quadrate) und *A. flavicollis* (Dreiecke) aus Silbertal und Kleinwalsertal, Vorarlberg, Österreich. Schwarze Quadrate bezeichnen *alpicola*-Paratypen aus dem Osterachtel, Allgäu, BRD. Die einzelnen Proben umfassen Tiere der Altersklassen 2–6

unabhängig bestimmt worden). Es ergibt sich eine nahezu überschneidungsfreie, nicht allometrisch bedingte Trennung der drei Punkteschwärme. Diese Maße am rostroventralen Schädelbereich (Abb. 5) sind – im Gegensatz etwa zur Hirnkapsel – sicher und reproduzierbar zu ermitteln, und sie sind auch an beschädigtem Sammlungsmaterial sowie an Schädelfragmenten aus Eulengewöllen meistens verfügbar.

Die Längen der Foramina incisiva von *alpicola* und *flavicollis* verhalten sich grundsätzlich wie das Diastemamaß, nur ist der Überschneidungsbereich größer. *A. sylvaticus* zeichnet sich durch lange Foramina incisiva aus, die bis zwischen die mesialen M1/-Wurzeln caudad reichen. Die Waldmaus besitzt durchschnittlich relativ längere Foramina incisiva als Alpenwaldmaus und Gelbhalsmaus.

Die Maße der Einzelzähne M1/ und M2/ spiegeln die Längenunterschiede der kompletten Zahnreihen zwischen den drei Arten wider. Der M3/ von *sylvaticus* hingegen ist durchschnittlich relativ kleiner als bei *alpicola* und *flavicollis* (Abb. 1–3, Tab. 1–2).

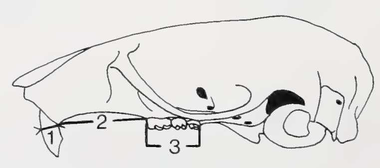


Abb. 5. Meßstrecken am *Apodemus*-Schädel zum Streudiagramm in Abb. 4. – 1 = Incisivendicke, 2 = Diastemalänge (Hinterrand Incisivenalveole – Vorderrand M1/-Alveole einer Körperseite), 3 = obere Zahnreihenlänge (nach Niethammer 1969, Abb. 1)

Molarenmorphologie

Die Höckermorphologie der Molaren stellt einen weiteren unabhängigen Merkmalskomplex dar. Michaux und Paquier (1974) fanden, daß der t9 (= distolabialer Höcker) am M2/ bei der Gelbhalsmaus häufig, bei der Waldmaus hingegen selten größenreduziert ist. Sie übertrugen diesen Befund auf pleistozäne europäische *Apodemus*-Populationen und schlossen, daß die Reduktion des t9 innerhalb der *flavicollis*-Entwicklungslinie ein abgeleitetes, modernes Merkmal darstellt. Die Ausprägung dieses Höckerchens am M2/ charakterisiert in unseren Proben nicht nur die Populationen von Wald- und Gelbhalsmaus, sie ist auch besonders kennzeichnend für *alpicola.*

Der t9 der Waldmaus ist ein rundlicher, ziemlich aufgeblähter Höcker, der sich in Occlusalansicht des Zahns nach labial vorwölbt (Abb. 3). Unter 46 als *sylvaticus* bestimmten Tieren befindet sich nur eines mit reduziertem t9.

Bei *flavicollis* liegt der t9 wohl noch höckerförmig vor, doch ist er mesiodistal gestreckt und wenig voluminös (Abb. 1). Der schlanke Höcker tritt an der Labialkontur des Zahns wenig hervor. Die Mehrzahl der Tiere zeigt diese typische Ausbildung; bei 6 Exemplaren ist der t9 mehr *sylvaticus*-ähnlich und bei einem mehr *alpicola*-ähnlich ausgebildet.

Der t9 von *alpicola* ist zu einem Kamm reduziert, in dessen Verlauf ein Höckerchen höchstens angedeutet ist (Abb. 2). Es gibt keine labiale Vorwölbung, sondern der M2/ verjüngt sich vom t6 an stetig nach distal. Von dieser kennzeichnenden Konfiguration weichen nur 5 (von 48) Tiere ab, deren t9 mehr in der für *flavicollis* bezeichnenden Weise ausgeprägt sind. Vier der 6 *alpicola*-Paratypen zeigen das typische Muster, und zwei besitzen schwach-höckerförmige t9.

Danksagung

Frau Angelika Helfricht (Senckenberg-Museum) fertigte die Zeichnungen an. Herr Dr. Herbert Tichy (Max-Planck-Institut für Biologie, Tübingen) bestimmte *alpicola*-Karyotypen, worüber er an anderer Stelle berichten wird. Herr Dr. Rainer Hutterer (Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn) lieh *alpicola*-Paratypen aus und half bei der Beschaffung von Burgscher Veröffentlichungen. Herr Prof. Dr. Jochen Niethammer (Zoologisches Institut der Universität, Bonn) las das Manuskript und gab Hinweise. Unterstützung bei der Feldarbeit erfuhren wir durch die Damen und Herren B. Boonsong, Petra Friesleber, J. Nabhitabatha und Hannes Storch. Allen sei hiermit herzlich gedankt.

Zusammenfassung

Die ursprünglich als hochmontane Vertikalrasse von *Apodemus flavicollis* angesehene Alpenwaldmaus erweist sich als eine morphologisch gut charakterisierbare Art, *Apodemus alpicola* Heinrich, 1952. Sie konnte in den Nordalpen (Kleinwalsertal und Montafon, Vorarlberg, Österreich) syntopisch neben *A. flavicollis* und *A. sylvaticus* nachgewiesen werden. Ihr Verbreitungsgebiet scheint auf die NW-Alpen beschränkt zu sein. Diagnostisch ist ein funktionell nicht korrelierter Merkmalskomplex von Färbung, Schädel- sowie Körperproportionen und Molarenmorphologie. Hiervon stellen die extreme Schwanzlänge, der verlängerte Gesichtsschädel und der reduzierte Höcker t9 des M2/ autapomorphe Merkmale dar, die *alpicola* gegenüber *sylvaticus* und *flavicollis* als höher spezialisiert ausweisen.

Literatur

Bauer, K.; Krapp, F.; Spitzenberger, F. (1967): Säugetiere aus Vorarlberg. Ann. naturhist. Mus. Wien. **70,** 55–71.

Gemmeke, H.; Niethammer, J. (1981): Die Waldmäuse *Apodemus sylvaticus* und *A. flavicollis* vom Monte Gargano (Süditalien). Z. Säugetierkunde **46,** 162–168.

Heinrich, G. (1951): Die deutschen Waldmäuse. Zool. Jb. Syst. Ökol. Geogr., **80,** 99–122.

— (1952): *Apodemus flavicollis alpicola,* N.N. J. Mammalogy **33,** 260.

Hutterer, R. (1984): I. Säugetiere. In: Die Wirbeltiersammlungen des Museums Alexander Koenigs. Ed. by G. Rheinwald. Bonn. zool. Monogr. **19,** 9–48.

Lehmann, E. von (1973): Die Waldmäuse des unteren Engadins, des Münstertales und Bergells. Jber. naturforsch. Ges. Graubünden **95,** 1–8.

LEHMANN, E. VON; KNECHT, H.-J. (1970): Die alpine Gelbhalsmaus (*Apodemus flavicollis alpicola* Heinrich, 1951) in Silum. Jb. hist. Ver. Fürstentum Liechtenstein **69**, 277–281.
MICHAUX, J.; PASQUIER, L. (1974). Dynamique des populations de Mulots (Rodentia, *Apodemus*) en Europe durant le Quaternaire. Bull. Soc. géol. France **16**, 431–439.
NIETHAMMER, J. (1969): Zur Frage der Introgression bei den Waldmäusen *Apodemus sylvaticus* und *A. flavicollis* (Mammalia, Rodentia). Z. zool. Syst. Evolutionsforsch. **7**, 77–127.
— (1978a): *Apodemus flavicollis* (Melchior, 1834) – Gelbhalsmaus. In: Handbuch der Säugetiere Europas. Ed. by J. Niethammer und F. Krapp. Wiesbaden: Akad. Verlagsges. Bd. **1** (I), 325–336.
— (1978b): *Apodemus sylvaticus* (Linnaeus, 1758) – Waldmaus. In: Handbuch der Säugetiere Europas. Ed. by J. Niethammer und F. Krapp. Wiesbaden: Akad. Verlagsges. Bd. **1** (I), 337–358.
REINWALDT, E. (1955): Zur Kenntnis der Gelbhalsmaus, *Apodemus flavicollis alpicola* Heinrich, 1951. Säugetierkdl. Mitt. **3**, 151–154.
STEINER, H. M. (1968): Untersuchungen über die Variabilität und Bionomie der Gattung *Apodemus* (Muridae, Mammalia) der Donau-Auen von Stockerau (Niederösterreich). Z. wiss. Zool. **177**, 1–96.
— (1978): *Apodemus microps* Kratochvil und Rosicky, 1952 – Zwergwaldmaus. In: Handbuch der Säugetiere Europas. Ed. by J. Niethammer und F. Krapp. Wiesbaden: Akad. Verlagsges. Bd. **1** (I), 359–367.

Anschrift der Verfasser: Dr. GERHARD STORCH und OTFRIED LÜTT, Forschungsinstitut Senckenberg, Senckenberganlage 25, D-6000 Frankfurt/M. 1

Z. Säugetierkunde 54 (1989) 347–359

ISSN 0044-3468

Electromorphic variation in selected South American Akodontine rodents (Muridae: Sigmodontinae), with comments on systematic implications

By J. L. Patton, P. Myers, and Margaret F. Smith

Museum of Vertebrate Zoology, University of California, Berkeley, and Museum of Zoology, University of Michigan, Ann Arbor, USA

Receipt of Ms. 15. 3. 1988

Abstract

Phylogenetic relationships among 13 species and 5 genera of South American muroid rodents of the Tribe Akodontini were examined by gel electrophoresis of 26 protein loci. The major findings include: 1. The genus *Microxus,* as represented by the type species *mimus,* cannot be distinguished from taxa of *Akodon* (subgenus *Akodon*). 2. *Bolomys,* as represented by the type species *amoenus,* is only slightly differentiated from *Akodon* (s. s.) and *Microxus* in both genetic distance and the number of uniquely defining alleles. 3. *Akodon (Chroeomys) jelskii* is very distinct from all other akodontines, with unique alleles at 9 of the 26 loci examined; it cannot be considered a close relative of *Akodon* (s. s.) and should be recognized at the generic level. And 4. *Lenoxus apicalis* is the most divergent akodontine with unique alleles at half of the loci studied; it does not form a clade with *Oxymycterus* as has been suggested by some authors.

Introduction

South American sigmodontine rodents (sensu Reig 1980) form a large array of some 50 genera and 200 species (Honacki et al. 1982) that presumptively comprise a single adaptive radiation (Hershkovitz 1962; but see Carleton 1980). These taxa have been grouped into seven or eight tribal categories (Hershkovitz 1962, 1966; Reig 1980, 1986, 1987; Vorontsov 1959) defined on a variety of craniodental, external, and soft anatomical features. Despite the diversity of recognized forms and the clarity of relationships suggested by the formal tribes, few of these taxa have been revised since their initial description, and groups are defined by few poorly studied and often contradictory characters. Much of our ignorance is due directly to the diverse nature of the group as a whole and to the fact that many taxa are known from but a few existing specimens. As a result, most studies have been forced to ignore many taxa except at the most superficial level, and the construction of well-supported phylogenetic hypotheses has been minimal at best. Students working on this general group of rodents have been forced to limit their perspectives to only selected members of any given tribe, or even species within any given supraspecific assemblage.

The Tribe Akodontini comprises one of the major subdivisions of the Sigmodontinae, as recognized by virtually all prior authors. This group is largely distributed through temperate South America and the Andean highlands, but members extend into the southern and western margins of the Amazon Basin and throughout the coastal and interior regions of southeastern Brazil. This is the group of interest to us in this report, and we follow for convenience Reig (1986, 1987) for its memberships (see Table 1).

The present paper defines relationships among selected generic or subgeneric units of this tribal group based on biochemical (= electromorphic) characters. In so doing, however, our data base suffers in the same way as that of all previous workers on neotropical sigmodontine rodents: less than one-half of the currently recognized supra-specific taxa of akodontines and fewer than one-third of the recognized species are

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5406-0347 $ 02.50/0

Table 1. **Supraspecific groups of akodontine rodents and number of recognized species (in parentheses) after Reig (1986)**

Taxa examined in this report are indicated by+

Tribe Akodontini
- genus *Akodon* (34)
  - subgenus *Akodon* (25)+
    - *Abrothrix* (6)
    - *Deltamys* (1)
    - *Hypsimys* (1)
    - *Chroeomys* (1)+
- genus *Oxymycterus* (9)+
  - *Bolomys* (6)+
  - *Chelemys* (4)
  - *Microxus* (3)+
  - *Notiomys*[1] (2)
  - *Blarinomys* (1)
  - *Podoxymys* (1)
  - *Lenoxus* (1)+
  - *Juscelinomys* (1)

[1] Pearson (1984) placed *N. valdivianus* in the monotypic genus *Geoxus* separate from *N. edwardsi.*

represented (Table 1). Thus, while we can provide some insights into the relationships among the taxa included herein for analysis, the more general questions regarding both the validity of an akodontine radiation separate from the other sigmodontine groups, as well as the secure placement of supraspecific taxa within the akodontines, must await more complete analyses.

Materials and methods

Tissue samples from 349 specimens representing six supraspecific taxa and 13 species of akodontine rodents were analyzed by horizontal starch-gel electrophoresis. These included seven species usually allocated to the nominant subgenus of *Akodon (aerosus baliolus, boliviensis, mollis, puer, subfuscus, torques,* and a unnamed form from central Peru); one species each of *Chroeomys (jelskii), Bolomys (amoenus),* and *Microxus (mimus);* the monotypic *Lenoxus apicalis,* and two species of *Oxymycterus (hiska* and *paramensis);* see Specimens Examined, below. The species representative of the taxa *Bolomys* and *Microxus* are the type species for those forms. Diagnoses and definitions of specific units recognized, particularly of those named forms usually associated with *Akodon "boliviensis"* (i. e., *boliviensis, puer,* and *subfuscus*), will be published separately.

Twenty-one enzymes and other proteins encoded by 26 presumptive structural gene loci were examined for all populations and taxa. Aqueous extracts of kidney were used for all systems examined. Alleles are designated by their mobility relative to the most common allele at each locus, which was set at 100. The enzymes and other proteins examined and the gel running conditions are given in Table 2. Estimates of genetic divergence of taxa were made using the distance measure of Rogers (1972). Patterns of phenetic similarity among taxa were examined by UPGMA clustering (Sneath and Sokal 1973); phylogenetic trees were constructed by the Wagner distance algorithm (Farris 1972), based on Rogers' D, and from individual character state matrices. Estimates of genic heterozygosity were obtained from the electromorphic genotypes by direct count and averaged across loci for population estimates of individual variability. All calculations of genetic distance and variability measures were performed using the BIOSYS-1 program (Swofford and Selander 1981) on an IBM 4341 mainframe computer, as were construction of UPGMA and Wagner trees. Cladistic analysis of character state matrices, based on the principle of maximum parsimony, was performed using PAUP (version 2.4; Swofford 1985) run on an IBM-PC/XT. In one set of analysis, loci were treated as characters and the observed allelic combinations within taxa were considered the states (following the rationale of Matson 1984, and Buth 1985; see example by Miyamoto 1983). In a second set of analyses, coding was by allelic state, with major alleles at each locus coded separately from minor ones. In the latter case, when no second allele was present in a given taxon, that state was considered as missing. Multistate characters in both analyses were treated as unordered rather than assuming a particular transformation series. Global branch swapping and the MULPARS option were used in PAUP to insure that all possible minimum length trees were found and examined. Wagner trees and those generated from PAUP were rooted either at the mid-point of the greatest patristic distance, or by using a combination of taxa designated as out-groups.

Specimens examined

All specimens are catalogued into the collection of either the Museum of Vertebrate Zoology, University of California (MVZ), or the Museum of Zoology, University of Michigan (UMMZ), as indicated.

Akodon (s. s.) – *aerosus baliolus:* Peru: Depto. Puno; [1] 4 km NE Ollachea, 2380 m (n = 44; MVZ); [2] 11 km NE Ollachea, 1880 m (n = 44; MVZ); [3] Abra Marracunca, 14 km W Yanahuaya, 2210 m (n = 28; MVZ). *boliviensis:* Peru: Depto. Puno; [4] 12 km S Santa Rosa [de Ayaviri], 3960 m (n = 19; MVZ). [5] 4.5 km W San Anton, 4000 m (n = 25; MVZ; [6] 6 km S Pucara, 3850 m (n = 14;

Table 2. **Enzymes and gel running conditions for samples of the akodontine rodents *Akodon* (s.s.), *Akodon (Chroeomys), Bolomys, Microxus, Lenoxus,* and *Oxymycterus***

Enzyme	Enzyme Commission Number	Locus Abbreviation	Electrophoretic Conditions[a]
Glycerol-3-phosphate dehydrogenase	1.1.1.8	Gpd	TC-8[2]
Sorbitol dehydrogenase	1.1.1.14	Sordh	TC-8[2]
Lactate dehydrogenase	1.1.1.27	Ldh-1, -2	TC-8[1]
Malate dehydrogenase	1.1.1.37	Mdh-1, -2	TC-8[2]
Malic enzyme	1.1.1.40	Me	TC-8[1]
Isocitrate dehydrogenase	1.1.1.42	Icd-1, -2	TC-8
6-phosphogluconate dehydrogenase	1.1.1.44	6Pgd	TM
Glyceraldehyde-3-phosphate dehydrogenase	1.2.1.12	Gapdh	TC-8[3]
Glutamate dehydrogenase	1.4.1.3	Gd	TM
Nadh-dehydrogenase	1.6.99.3	Nadh-dh	TC-8
Superoxide dismutase	1.15.1.1	Sod	TC-8[3]
Purine nucleoside phosphorylase	2.4.2.1	Np	LiOH
Aspartate aminotransferase	2.6.1.1	Got-1, -2	TC-8[1]
Creatine kinase	2.7.3.2	Ck-1, -2	TC-8[1]
Phosphoglucomutase	2.7.5.1	Pgm	PGI Phos
Peptidase	3.4.11	Pep-D[b]	Poulik
Peptidase	3.4.11	Pep-B[b]	Poulik
Adenosine deaminase	3.5.4.4	Ada	PGI Phos
Mannose-phosphate isomerase	5.3.1.8	Mpi	TC-7
Glucose-phosphate isomerase	5.3.1.9	Gpi	PGI Phos
Albumin	—	Alb	LiOH

[a] TC-8[1] – Tris-Citrate, pH 8.0, 130 v, 4 hr
TC-8[2] – Tris-Citrate, pH 8.0, 130 v, 4 hr, NAD added to gel
TC-8[3] – Tris-Citrate, pH 8.0, 130 v, 4 hr, NAD and 2-mercapto-ethanol added to gel
TC-7 – Tris-Citrate, pH 7.0, 180 v, 3 hr
LiOH – Lithium Hydroxide, pH 8.1, 300 v, 3 hr, glycerine added to gel
PGI Phos – PGI Phosphate, pH 6.7, 130 v, 4 hr, NADP added to gel
Poulik – "Poulik" system of Selander et al. (1971), adjusted to pH 9.1, 250 v, 3 hr
TM – Tris-Maleic Acid EDTA, pH 7.4, 100 v, 4 hr.
[b] Pep-D = phenylalanine-proline substrate; Pep-B = leucine-glycine-glycine substrate.

MVZ). *mollis:* [7] Peru: Depto. Junin; 16 km E Palca, 2540 m (n = 16; MVZ). *puer:* Peru: Depto. Puno; [8] 12 km S Santa Rosa [de Ayaviri], 3960 m (n = 6; MVZ); [9] 6 km S Pucara, 3850 m (n = 23; MVZ); [10] 3.6 km W Munani, 3950 m (n = 5; MVZ). *subfuscus:* Peru: Depto. Cusco; [11] 32 km NE Paucartambo, 3140 m (n = 10; MVZ, UMMZ); [12] 20 km N Paucartambo, 3580 m (n = 10; MVZ); [13] Depto. Puno; 6.5 km SW Ollachea, 3350 m (n = 35; MVZ). *torques:* [14] Peru: Depto. Cusco; below Abra Malaga, 90 km SE Quillabamba, 3450 m (n = 13; MVZ, UMMZ). sp.?: [15] Peru: Depto. Junin; 22 km NE La Oroya, 4040 m (n = 7; MVZ).

Akodon (Chroeomys) jelskii: Peru: Depto. Junin; [16] 22 km NE La Oroya, 4040 m (n=3; MVZ); Depto. Puno; [17] 12 km S Santa Rosa [de Ayaviri], 3960 m (n=1; MVZ); [18] 4.5 km W San Anton, 4000 m (n=3; MVZ); [19] 6.5 km SW Olachea, 3350 m (n=15; MVZ).

Bolomys amoenus: Peru: Depto. Cusco; [20] 20 km N Paucartambo, 3580 m (n=1; MVZ); Depto. Puno; [21] 12 km S Santa Rosa [de Ayaviri], 3960 m (n=7; MVZ).

Microxus mimus: Peru: Depto. Puno; [22] Agualani, 9 km N Limbani, 2840 m (n=7; MVZ); [23] Abra Marracunca, 14 km W Yanahuaya, 2210 m (n=2; MVZ).

Oxymycterus hiska: Peru: Depto. Puno; [24] Abra Marracunca, 14 km W Yanahuaya, 2210 m (n=3; MVZ).

Oxymycterus paramensis: Peru: Depto. Cusco; [25] 55 km N Calca (by road), 3560 m (n=2; UMMZ).

Lenoxus apicalis: Peru: Depto. Puno; [26] Abra Marracunca, 14 km W Yanahuaya, 2210 m (n=6; MVZ).

Results

The purpose of this paper is to examine patterns of electromorphic variation among taxa assignable to the akodontine group of Neotropical cricetid rodents; it is not our intention to describe in detail such variation as we know exists within species over their sampled geographic ranges. As a consequence, the measures reported below, and in the accompanying tables, are summaries averaged across the population samples of each species for which we have data (see Specimens Examined, above).

Variation within taxa

Values for the average number of alleles per locus (A), percent of loci polymorphic per population (P), and proportion of loci heterozygous per individual per population sampled (H) are provided in Table 3. The average species of akodontine rodent examined in this

Table 3. **Measures of electromorphic variability within 13 species and six supraspecific taxa of akodontine rodents**

Taxon	N_p	N_i	A	P	H
Akodon (Akodon) aerosus	3	116	1.2	11.0	0.022
boliviensis	3	58	1.3	20.9	0.067
mollis	1	16	1.2	15.4	0.026
puer	3	34	1.3	21.3	0.069
subfuscus	3	55	1.2	16.1	0.055
torques	1	13	1.1	7.7	0.042
sp.	2	9	1.1	7.7	0.011
weighted average			1.2	15.0	0.043
Akodon (Chroeomys) jelskii	8	34	1.2	15.2	0.071
Bolomys amoenus	2	8	1.1	10.5	0.024
Microxus mimus	2	9	1.0	3.0	0.009
Oxymycterus hiska	1	2	1.1	11.5	0.038
paramensis	1	3	1.0	3.8	0.038
Lenoxus apicalis	1	6	1.1	7.7	0.013
grand mean			1.15	11.68	0.0373

N_p = number of populations; N_i = number of individuals; A = average alleles per locus; P = percent loci polymorphic (95 % criterion); and H = proportion of loci heterozygous per individual.

report is polymorphic at 11.68 percent of its loci, and the average individual is heterozygous for 3.73 percent of its loci. These are somewhat lower values than are typical for rodents as a group (see reviews by Nevo 1978; Nevo et al. 1984). Nevertheless, there is a wide variance in these values across all taxa examined, with P and H values varying from 3.0 to 21.3 and from 0.9 to 7.1 percent, respectively. In general, species of *Akodon* (s.s.) exhibit more variability on average than do those of other genera, and within *Akodon*, those species inhabiting the Altiplano (*boliviensis puer*, and *subfuscus*) exhibit about twice the degree of variability within populations as do those occurring on the eastern forested slopes of the Andes (*aerosus*, *mollis*, and *torques*; see Table 3).

Differentiation among taxa

A summary of genetic differentiation within and among suprageneric taxa of akodontine rodents is presented both as a matrix of Rogers' genetic distances (Table 4) and as a list of

Table 4. **Matrix of Rogers' genetic distances (DR; Rogers 1972) among populations and taxa of akodontine rodents**

	AAab	AAb	AAm	AAp	AAs	AAt	AAsp	ACj	Ba	Mm	Oh	Op	La
A(A)ab	.023	.090	.097	.125	.113	.141	.141	.530	.304	.128	.424	.436	.566
b		.027	.162	.148	.151	.190	.188	.531	.297	.174	.416	.455	.597
m			—	.197	.178	.081	.211	.539	.305	.188	.402	.431	.538
p				.030	.083	.231	.160	.516	.344	.201	.421	.403	.570
s					.035	.225	.173	.521	.344	.191	.423	.408	.568
t						—	.242	.497	.305	.250	.403	.447	.584
sp.							—	.571	.410	.226	.452	.458	.657
A (C) j								.075	.492	.548	.551	.636	.764
Ba									.014	.346	.350	.464	.635
Mm										.060	.438	.435	.576
Oh											—	.337	.639
Op												—	.645
La													—

Average distances among populations of a single species are given on the diagonal where more than one sample was examined

uniquely defining alleles per taxon (Table 5). The major conclusions obvious from these data are the following:

1. The samples of populations of any single species are relatively homogeneous across geography (Table 4). These values are typical of infraspecific differentiation observed for most species of cricetid rodents (Avise 1976; Avise and Aquadro 1982). For example, the samples of *A. (C.) jelskii* encompass the entire geographic range of this species in Peru, including several very well-marked subspecies (see Sanborn 1947), yet the degree of genic differentiation is small (mean $D_R = 0.075 \pm 0.004$ standard error; Table 4). Nonetheless, with the limited sampling available, substantive differences do exist in the comparison of differentiation among samples for species inhabiting virtually the same geographic ranges. For example, the samples of *A. aerosus baliolus* come from the middle elevation tributaries of the Rio Inambari in southeastern Peru, while those of *Microxus mimus* come from the upper parts in the same drainage. The latter taxon, however, exhibits nearly three times the degree of differentiation among populations as does the former ($D_R = 0.060$ versus 0.023 ± 0.003 standard error; Table 4).
2. The differentiation that is present between most pairs of *Akodon* species, including *Microxus*, is due to fixed differences for alleles that are otherwise broadly distributed among the total set of species examined in this group. For example, sympatric *boliviensis* and *puer* are distinguished by the GOT-1^{100} and GOT-$1^{162, 131}$ alleles, respectively. However, *aerosus, mollis, torques,* and *Microxus* all share the 100 allele, and *subfuscus* shares both 162 and 131 alleles. On the other hand, *boliviensis* and *puer* share the PGI^{167} allele while the others, including *Microxus*, have the 100 allele (Table 5).
3. Differentiation among sampled species within the supraspecific taxon *Akodon* (s.s.) is relatively slight. The average distance among all populations of the seven species is 0.158 (range 0.081–0.242, see Table 4). With the single exception of the unnamed species from central Peru, no alleles are uniquely fixed for any of these species (Table 5). On the other hand, the two species of *Oxymycterus* are strongly differentiated, with $D_R = 0.337$ (Table 4). Five uniquely fixed alleles in *O. paramensis* and the two in *O. hiska* are responsible for most of this measured distance (Table 5).
4. Not all of the currently recognized genera (Honacki et al. 1982; Reig 1987) are composed of genically uniform and similar species relative to others. For example, *Microxus mimus* is much more similar to *Akodon* (s.s.) than is *Akodon (Chroeomys)*

Table 5. **Alleles segregating at 26 electromorphic loci for 13 taxa of akodontine rodents**
Alleles are identified by relative mobility, as measured from the origin, with the common allele set at 100

			Akodon (Akodon)					*(Chroeomys)*	*Bolomys*	*Microxus*	*Oxymycterus*		*Lenoxus*
Locus	*aerosus*	*boliv.*	*mollis*	*puer*	*subfuscus*	*torques*	Species	*jelskii*	*amoenus*	*mimus*	*hiska*	*paramensis*	*apicalis*
Ldh-1	100	108, 100	100	100	100	100	100, 92	100	100	100	100	100	100
Ldh-2	100, 82	100	100	100	100	100	100	111	100	100	79	100	100
Ck-1	100	100, 74	100	100	100	100	132	100	100	100	100	100	100
Ck-2	100	100	100	100	100	100	100	143, 100	100	100	100	43	100
Got-1	100	100	100	162, 131	162, 131	100	131	108	100	100	123	142	85
Got-2	100, 43	100	100	100	100	100	100	86	100, 71	100	100	100	100
Icd-1	105, 100	100	144, 100	100, 82	118, 100	127, 100	77	109, 86	100	100	91	91	91
Icd-2	100	100	100	100	150, 100	100	100	100	100	100	100	100	108
Mpi	100, 76	100	100	124, 100 88	124, 100	100	100	129, 100	124	100	135, 100	100	153
Gpd	100	100, 71 57	121	100, 91	100, 57	121	100	43	121	100	121	157	78
Mdh-1	112, 100	100	100	100	100	100	100	100	100	100	100	100	100
Mdh-2	100	100, 33	100	100	100	100	100	89	100	100	100	100	100
Sdh	100, 21	100	100	100	100	100	100	100, 29	100	100	100	100	14
6Pgd	100	117, 100	100	100	100	100	100	117, 100	100	100	100	100	108
Pgi	100	167, 100	100, 67	167, 100	100	100	100	67, 17	100, 67	100	67	100	83
Ada	100, 88	100, 88 77	100, 88	100, 88 77	100, 88, 77	100	107, 100	112	97	107, 100	100, 87	81	95, 86
Pgm	138, 100	150, 100	100	100	150, 100, 75	100	100	100, 63	100	100	100	100	100
Sod	100	100	100	100	100	100	100	100	100	100	100	100	100
Ga3Pdh	163, 100	100	163	100	100	163	100	75	100	100	100	100	163
Np	100, 75	100, 63	100	100, 63	100	75	100	100, 75, 38	112	100	112	112, 88	100, 75
Alb	100	100	100	100	100	100	100	94	106	94	106, 103	106	91
Gd	100	100	100	100	100	100	100	100	100	110, 100	100	100	105
Nadh-dh	100	157, 100	100	157,100	157, 100	100	100	171	100	100	14	14	143
Me-2	100	122, 100	117, 100	100	100	100	100	100	100, 78	72	111	111	144
Pap	100	100	100	100	100	100	100	100	100	100	100	107	113
Lgg	100	100	100	100	100	100, 75	100	91	91	100	93	93	93
Total # alleles	36	39	30	36	36	28	28	35	29	28	29	27	28
Total unique alleles	7	4	2	2	3	2	3	16	3	2	5	6	14
Total unique fixed	0	0	0	0	0	0	2	9	1	1	2	5	13[a]

[a] Unique, but polymorphic alleles at single loci counted as one.

jelskii by a factor of over two (mean *Microxus-Akodon* D_R = 0.194 whereas *Microxus-Chroeomys* = 0.529 and *Akodon-Chroeomys* = 0.548; Table 4).

5. Moreover, the subgenus *Chroeomys* is more strongly differentiated from *Akodon* (s.s.) than is *Bolomys amoenus*, which has been accorded generic status by many modern authors (see REIG 1987, and MACEDO and MARES 1987, for the history of the concept). It is even more strongly differentiated from *Akodon* (s.s.) than is *Oxymycterus* (mean D_R = 0.429; Table 4). *Chroeomys* is characterized by 17 unique alleles, nine of which are fixed (Table 5).
6. *Lenoxus* is the most strongly differentiated supraspecific taxon, with genetic distances to all others ranging from 0.538 to 0.764. Moreover, it is as divergent in comparison to *Oxymycterus* as it is to the other sampled genera (Table 4). These very large genetic distances are the result of 14 unique alleles (out of a total of 28) at 13 of the 26 loci examined; that is, fully 50 percent of the measured genome of *Lenoxus* is unique.
7. These taxa of akodontines are generally characterized by alleles either that are broadly shared among taxa or that uniquely define them. For example, four of the 26 loci examined exhibit a common allele shared by all taxa (Ldh-1, Mdh-1, Pgm, and Sod) and an additional 11 loci show a common allele shared by more than 10 of the taxa examined (Ldh-2, Ck-1, -2, Got-2, Icd-2, Mdh-2, Mpi, Sdh, 6Pgd, Pap, and Gd). On the other hand, of the total of 118 alleles detected, 68 of these (58.6 percent) are unique to single species.

Relationships among akodontine rodents

The relationships among this set of akodontine taxa suggested by these data are provided in figures 1 and 2 which represent, respectively, phenetic and phyletic perspectives based on genetic distances. The topologies of these trees are strongly concordant, with a single exception. In both cases, *Microxus* is placed within the complex of species that represent *Akodon* (s.s.), and *Akodon (Chroeomys)* is placed outside of a complex that includes *Akodon* (s.s.) and *Bolomys amoenus*. *Lenoxus* is placed outside of all the other taxa based on mid-point rooting; it does not form an identifiable unit with *Oxymycterus*. The only topological disagreement between these two views of relationships resides in the placement of the unnamed species of *Akodon* (s.s.) from central Peru. In the phenogram, it is the most differentiated member of *Akodon* (s.s.), while in the WAGNER tree it is coupled with *subfuscus* and *puer* relative to all others. Note that in the WAGNER tree, the branch lengths leading to the terminal taxa are approximately the same, indicating that the degree of accumulated molecular divergence has been relatively constant across lineages. Only *Lenoxus* seems to stand apart, but, as its placement is based on mid-point rooting, the actual length of the branch leading to it remains uncertain.

The high proportion of either broadly shared (= common) or unique alleles makes the documentation of any internal branching hierarchy among these taxa difficult at best (Fig. 3). For example, there are no alleles that uniquely define the seven species of *Akodon* (s.s.) as a group relative to other supraspecific taxa, and only three that so define *Oxymycterus* (Table 5). On the other hand, *Lenoxus* has uniquely fixed alleles at 50 percent of the loci examined (13/26), and *Chroeomys* is similarly distinctive at 34.5 percent of its loci (9/26). As a result, any character-state analysis will produce a large number of equally parsimonious trees, and resolution of relationships among these taxa supportive of the trends observed in the phenetic and WAGNER distance procedures is not possible. Results of the various PAUP analyses, however, are informative. For example: 1. Every tree, regardless of the specified out-group taxon (or group of taxa), places *Microxus* as a member of a clade otherwise composed only of species of *Akodon* (s.s.). 2. It is not possible to identify *Microxus* as part of an out-group relative to *Akodon* (s.s.) without making the specified in-group polyphyletic (see also HINOJOSA et al. 1987). 3. Equal length trees are produced when *Lenoxus*, *Oxymycterus*, *Bolomys*, or *Chroeomys* are designated as

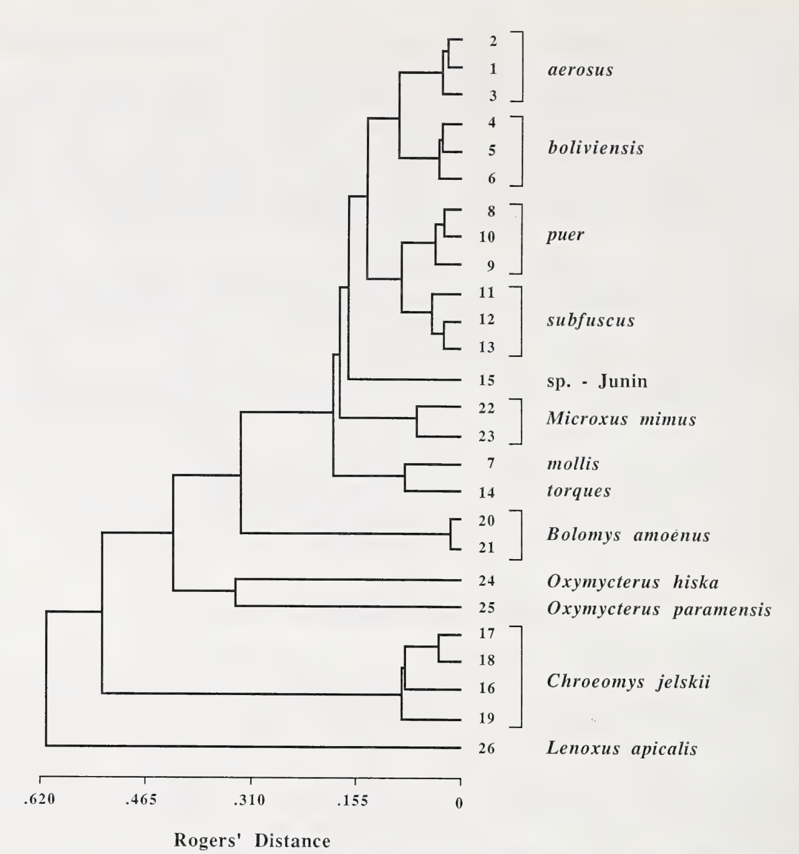


Fig. 1. UPGMA dendrogram of ROGERS' (1972) genetic distance (D_R) for thirteen species and six supraspecific groups of akodontine rodents. Taxa not identified to genus are all members of *Akodon* (s. s.). Geographic localities for each taxon are indicated by number, as in the Specimens Examined section. Cophenetic correlation coefficient = 0.982

the out-group taxon. But, 4. a combination of *Oxymycterus* and *Lenoxus* (members of HERSHKOVITZ' [1966] oxymycterine group) cannot be specified as an out-group together while, at the same time, retaining the remaining taxa as a monophyletic in-group (contra the more limited analysis presented in HINOJOSA et al. 1987).

A concensus tree summarizing relationships among these six supraspecific taxa of akodontine rodents is given in Fig. 3. *Akodon* (s.s.) and *Microxus* are linked by two uniquely shared alleles, and a clade composed of all taxa with the exception of *Lenoxus* is identifiable by three shared alleles. However, it is not possible on the basis of character states alone to link *Bolomys, Chroeomys*, and *Oxymycterus* other than in a multichotomous fashion. Although these taxa exhibit quite different overall genetic distances both to *Akodon* (s.s.) and *Microxus* or to *Lenoxus*, these distances are the result of unique alleles along each branch, not shared ones that couple them in some hierarchical fashion.

Discussion

Akodontine rodents comprise a group of 10 genera and some 62 species (following REIG 1986). The most polytypic of these is the genus *Akodon*, for which REIG (1986) recognizes

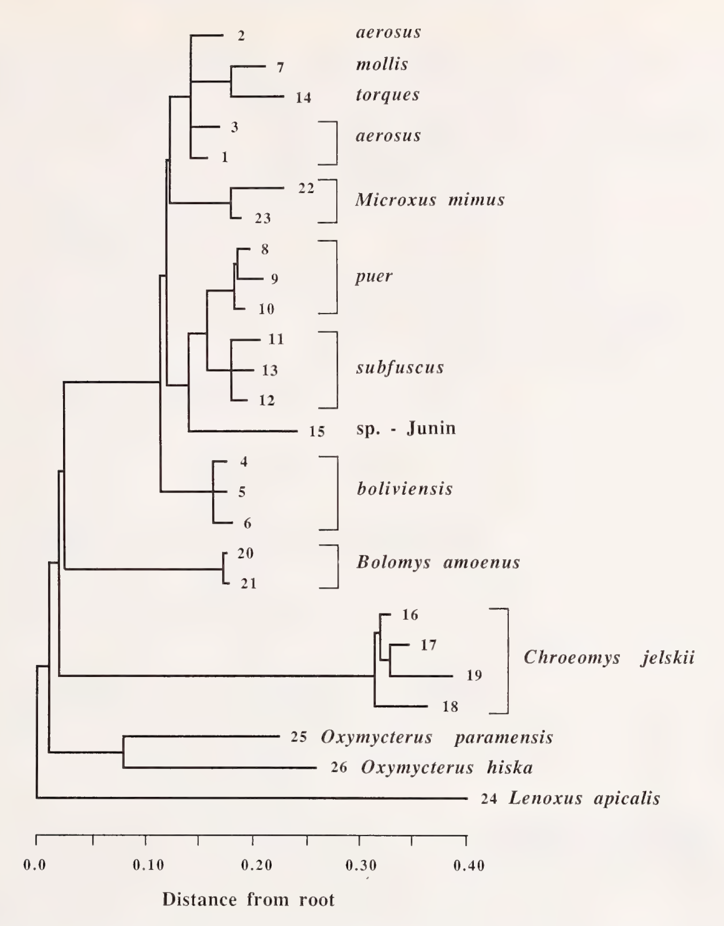


Fig. 2. Distance WAGNER tree based on ROGERS' genetic distance for thirteen species and six supraspecific groups of akodontine rodents (see Fig. 1). The tree was rooted by designating *Lenoxus* as an out-group taxon. Total tree length = 2.260; cophenetic correlation coefficient = 0.993

five subgeneric assemblages (*Akodon* s.s., *Abrothrix, Deltamys, Hypsimys,* and *Chroeomys*). While authors vary as to the explict taxa they recognize, and at what categorical level, no author has seriously questioned the monophyletic nature of the group. Rather, discussions associated with the akodontines have focused on 1. how many subgeneric groups of *Akodon* to recognize, and whether some of these should be recognized at the generic level; 2. whether *Zygodontomys* is an akodontine or not, and 3. whether the oxymycterines should be segregated as a group distinct from other akodontines, but annectant to them (e.g. HERSHKOVITZ 1966). REIG (1987) provides a valuable synopsis of the history of the concept of the akodontines, and there is no need to repeat these remarks here. HINOJOSA et al. (1987) review the question of an oxymycterine as opposed to an akodontine group and conclude that the definition of such is inconclusive with present information.

With the data presented above, we cannot address the issue of monophyly of an akodontine clade relative to other sigmodontines, as the analysis did not include any taxa outside of the akodontines as defined by REIG and other workers. We can, however, evaluate a set of hypotheses that previous authors have presented relative to relationships

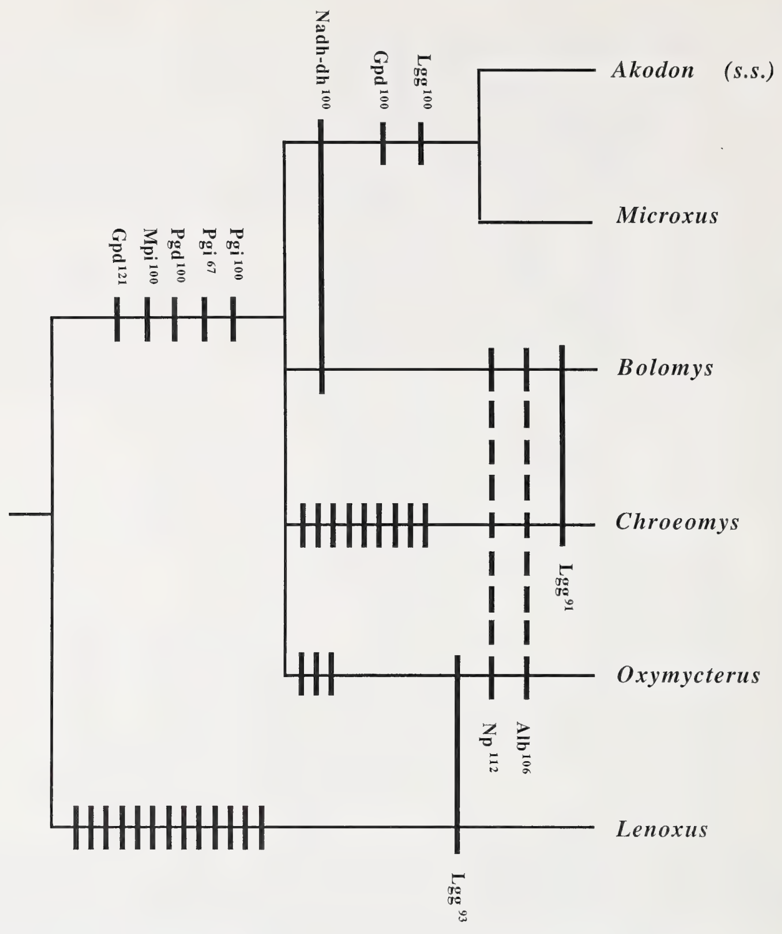


Fig. 3. A generalized cladogram for six supraspecific groups of akodontine rodents based on electromorph (= allele) distribution patterns. Alleles uniting pairs or groups of taxa are identified; those that uniquely define terminal taxa are indicated only as horizontal bars. See text for further discussion, and Table 5 for a list of allelic states for each taxon

within the akodontine group and, based on these evaluations, we can provide arguments for the hierarchical classification of the taxa that we have examined.

As Reig's (1987) synopsis of the history of the concept of the Akodontini reveals, there has been, and continues to be, much confusion as to the number of supraspecific units and of their suggested relationships. As a case in point, Hershkovitz (1966) included *Microxus* with *Abrothrix* in an oxymycterine group apart from the akodonts, while most prior and subsequent authors continue to recognize *Microxus* as a separate genus of akodonts and *Abrothrix* as a subgenus of *Akodon*. A similar history surrounds the supraspecific taxon *Bolomys* (see Macedo and Mares 1987). This state of affairs exists because supraspecific taxa (generic and subgeneric groups) are poorly defined within the akodontines. It is frankly not clear whether the lack of definition is real, in that it reflects only subtle differences among clades that diverged nearly simultaneously from a common ancestor resulting in taxa composed of a combination of primitively shared and uniquely derived characters, or whether the lack of a good definition now simply results from the fact that

no thorough analyses of character variation has been accomplished for all presumptive members of the group. For example, GARDNER and PATTON's (1976) compilation of chromosomal data provides a systematic view for only 5 of the 15 supraspecific groups of REIG (1986, 1987). Similarly, CARLETON's (1973) analysis of stomach morphology among the New World cricetines involves only four of these groups; and VOSS and LINZEY's (1981) study of the male reproductive tract examines but six. As useful as these studies are, the paucity of the available data means that substantive conclusions about supraspecific limits cannot be drawn as yet.

Our study suffers from the same faults as prior ones; it encompasses an inadequate number of akodontine taxa for a full view of the diversity of the group, and of the phyletic relationships of its components. Nevertheless, there are some firm conclusions that come from these data with regard to the hierarchical placement of several of the supraspecific taxa generally placed within this group. These inlcude:

1. *Microxus* (as represented by topotypic material of the type species, *mimus*) is at best a sister group to *Akodon* (s.s.), and perhaps will be found to have its place within that group. Certainly, it is more closely related to *Akodon* than is either *Chroeomys* or *Bolomys*, two supraspecific taxa that have been recognized as genera or subgenera of *Akodon* (THOMAS 1916, 1918; ELLERMAN 1941). The suggestion of HERSHKOVITZ (1966) that *Microxus* is an oxymycterine, not an akodont, is certainly not supported by the electromorphic data presented here or by a review of morphological characters (see HINOJOSA et al. 1987). His further argument that *Microxus* is an *Abrothrix* cannot be evaluated here; no other taxa allocated to *Abrothrix* were examined by us. We suspect, based on examination of specimens of the three species usually allocated to *Microxus* (*mimus,* the type species, *latibricola*, and *bogotensis*) is that *mimus* bears no relationship to the other two. Hence, the opinions of authors, such as REIG (1987), that *Microxus* stands apart from other akodontines may well rest on their view that *bogotensis* adequately represents the genus. It probably does not, and these species should be redefined relative to *Microxus mimus*.
2. *Chroeomys* is at least as equally divergent as is *Bolomys* (as represented by the type species *amoenus*) and, apparently, *Oxymycterus* relative to *Akodon* (s.s.). If *Bolomys* is to be recognized at the generic level, as most recent authors have done (see REIG 1987, for formal diagnosis of the genus *Bolomys*), then so must *Chroeomys* if paraphyletic taxa are to be disallowed, a philosophy to which we agree. This view is consistent with a general overview of the morphological and chromosomal position of *Chroeomys* made recently by SPOTORNO (1986).
3. *Lenoxus* is the most strongly differentiated taxon examined here, and it does not have a close relationship with any other akodontine. Judging by the number of unique alleles, it has had a long history of separation. Certainly, it is not close to *Oxymycterus* (following HERSHKOVITZ 1966), and it cannot be considered just a large version of that genus (REIG 1980, 1987). Nevertheless, it does have the highly specialized discoglandular stomach, very similar in morphology to that of *Oxymycterus* as described by CARLETON (1973; PATTON unpubl. data). Comparisons to genera outside of the akodontines are necessary to determine if *Lenoxus* and *Oxymycterus* are sister-taxa; i.e., its relationships may lie with *Oxymycterus*, but, if so, the divergence was near the basal radiation of the entire group.
4. The addition of other taxa, both the remaining genera and subgenera as well as a greater representation of speciose genera such as *Oxymycterus* and *Akodon*, will undoubtedly help resolve the relationships suggested herein. However, the general patterns detailed here suggest that most genera had their origins nearly simultaneously from a common ancestral stock(s). This view is supported by the dual facts that these taxa share a large number of alleles across the loci examined while simultaneously they are individually characterized by unique alleles. The pattern of electromorphic divergence, therefore,

mirrors the conclusion of Voss and Linzey (1981) regarding features of the male reproductive tract: evolution within the South American cricetines, as exemplified by the akodontines discussed herein, has likely been by ". . . rapid cladistic proliferation".

Acknowledgements

We thank Monica Frelow and Jennifer Talbot for help with all aspects of the laboratory analysis, and Carol Patton, John Cadle, Bob Jones, Michael Nachman, and Elena Vivar P. for aid in the collection of specimens. Oliver Pearson read an early draft of the paper and improved its contents based on his extensive personal experience with these rodents. Logistical support in Peru was provided by Tony Luscombe, Mari Figueroa, Renato Marin, and the Museo Historia Natural "Javiar Prado", and collecting permits were kindly supplied by the Ministerio de Agricultura, Lima. Financial support was provided by the National Geographic Society, the National Science Foundation, the Museum of Vertebrate Zoology, and the Rackham Foundation of the University of Michigan.

Zusammenfassung

Elektrophoretische Variabilität bei ausgewählten südamerikanischen akodontinen Nagetieren (Muridae: Sigmodontinae), mit Anmerkungen über Folgerungen zur Systematik

Die phylogenetischen Beziehungen zwischen 14 Arten aus 5 Gattungen südamerikanischer muroider Nager der Tribus Akodontini wurden mit Hilfe des gelelektrophoretischen Vergleichs von 26 Proteinen untersucht. Die Hauptergebnisse sind: 1. *Microxus mimus*, die Typus-Art der Gattung *Microxus*, kann nicht von *Akodon*-Arten aus der Untergattung *Akodon* unterschieden werden. 2. *Bolomys amoenus* unterscheidet sich genetisch nur wenig von *Akodon* (s.s.) und *Microxus mimus*. 3. *Akodon (Chroemys) jelskii* weicht sehr von allen anderen Akodontinen ab. Die Art besitzt an 9 der 26 untersuchten Loci nur bei ihr gefundene Allele. Sie ist mit Arten der Gattung *Akodon* (s.s.) nicht eng verwandt und sollte in eine eigene Gattung gestellt werden. 4. Am stärksten differenziert ist *Lenoxus apicalis*. 13 der 26 untersuchten Loci besitzen ausschließlich eigene Allele. Entgegen der Ansicht mancher Autoren bildet *Lenoxus* mit *Oxymycterus* keine monophyletische Gruppe.

Resumen

Las relaciones filogenéticas entre 13 especies y 5 generos de roedores muroideos sudamericanos de la Tribu Akodontini se examinaron mediante electroforesis de 26 loci proteicos. Los principales hallazgos incluyen: 1. El género *Microxus*, representado por la especie tipo *mimus*, es indistinguible de los taxa de *Akodon* (subgenero *Akodon*). 2. *Bolomys*, representado por la especie tipo *amoenus*, sólo se diferencia ligeramente de *Akodon* (s.s.) y *Microxus*, tanto en distancia genica como en el número de alelos diagnósticos. 3. *Akodon (Chroeomys) jelskii* es muy diferente de todos los otros akodontinos, con alelos diagnósticos en 9 de los 26 loci examinados; este taxón no puede considerarse pariente cercano de *Akodon* (s.s.) y debería reconocerse al nivel de género. Y 4. *Lenoxus apicalis* es el akodontino mas divergente con alelos diagnósticos en la mitad de los loci estudiados; este taxón no forma un clado con *Oxymycteros* como algunos autores han sugerido.

Literature

Avise, J. C. (1976): Genetic differentiation during speciation. In: Molecular evolution. Ed. by F. J. Ayala. Sinauer Assoc. Inc., Sunderland, MA, pp. 106–122.

Avise, J. C.; Aquadro, C. F. (1982): A comparative summary of genetic distances in vertebrates. In: Evolutionary Biology. Ed. by M. K. Hecht, B. Wallace and G. T. Prance. New York: Appleton-Century-Crofts. pp. 151–185.

Buth, D. G. (1984): The application of electrophoretic data in systematic studies. Ann. Rev. Ecol. Syst. **15**, 501–522.

Carleton, M. D. (1973): A survey of gross stomach morphology in New World Cricetinae (Rodentia, Muroidea), with comments on functional interpretations. Misc. Publ. Mus. Zool., Univ. Mich. **146**, 1–43.

Ellerman, J. R. (1941): The families and genera of living rodents. Family Muridae. British Mus. Nat. Hist. Vol. II.

Farris, J. S. (1972): Estimating phylogenetic trees from distance matrices. Amer. Nat. **106**, 645–668.

Gardner, A. L.; Patton, J. L. (1976): Karyotypic variation in oryzomyine rodents (Cricetinae) with

comments on chromosomal evolution in the Neotropical cricetine complex. Occas. Papers Mus. Zool., La. State Univ. **49**, 1–48.

Hershkovitz, P. (1962): Evolution of Neotropical cricetine rodents (Muridae), with special reference to the phyllotine group. Fieldiana: Zoology **46**, 1–524.

— (1966): South American swamp and fossorial rats of the scapteromyine group (Cricetinae, Muridae) with comments on the glans penis in murid taxonomy. Z. Säugetierkunde **31**, 81–149.

Hinojosa, P. F.; Anderson, S.; Patton, J. L. (1987): Two new species of *Oxymycterus* (Rodentia) from Peru and Bolivia. Amer. Mus. Novitates No. **2898**, 17 pp.

Honacki, J. H.; Kinman, K. E.; Koeppl, J. W. (1982): Mammal species of the world. Lawrence, Kansas: Allen press.

Macedo, R. H.; Mares, M. A. (1987): Geographic variation in the South American cricetine rodent *Bolomys lasiurus*. J. Mammalogy **68**, 578–594.

Matson, R. H. (1984): Application of electromorphic data in avian systematics. Auk **101**, 717–729.

Miyamoto, M. M. (1983): Biochemical variation in the frog *Eleutherodactylus bransfordii*: geographic patterns and cryptic species. Syst. Zool. **32**, 43–51.

Nevo, E. (1978): Genetic variation in natural populations: patterns and theory. Theor. Pop. Biol. **13**, 121–177.

Nevo, E.; Beiles, A.; Ben-Shlomo, R. (1984): The evolutionary significance of genetic diversity: ecological, demographic, and life history correlates. In: Evolutionary dynamics of genetic diversity. Ed. by G. S. Mani. Lecture Notes Biomath. vol. **53**.

Pearson, O. P. (1984): Taxonomy and natural history of some fossorial rodents of Patagonia, southern Argentina. J. Zool., London, **202**, 225–237.

Reig, O. A. (1980): A new fossil genus of South American cricetid rodents allied to *Wiedomys*, with an assessment of the Sigmodontinae. J. Zool., London, **192**, 257–281.

Reig, O. A. (1986): Diversity patterns and differentiation of high Andean rodents. In: High Altitude Tropical Biogeography. Ed. By F. Vuilleumier and M. Monasterio. Oxford: Oxford University Press. pp. 404–439.

Reig, O. A. (1987): An assessment of the systematics and evolution of the Akodontini, with the description of new fossil species of *Akodon* (Cricetidae: Signodontinae). In: Studies in Neotropical Mammalogy: Essays in honor of Philip Hershkovitz. Ed. by B. D. Patterson and R. M. Timm. Fieldiana: Zoology, new ser. **39**, 346–399.

Rogers, J. S. (1972): Measures of genetic similarity and genetic distance. Univ. Texas Publ. **7213**, 145–153.

Sanborn, C. C. (1947): Geographic races of the rodent *Akodon jelskii*. Fieldiana: Zoology **31**, 137–142.

Sneath, P. H. A.; Sokal, R. R. (1973): Numerical taxonomy. The principles and practice of numerical classification. San Francisco: W. H. Freeman.

Spotorno, A. O. (1986): Systematics and evolutionary relationships of Andean phyllotine and akodontine rodents. Unpubl. PhD dissertation, Univ. California, Berkeley.

Swofford, D. L. (1985): PAUP. Phylogenetic analysis using parsimony, version 2.4. Champaign, Illinois: Illinois Nat. Hist. Survey.

Swofford, D. L.; Selander, R. B. (1981): A computer program for the analysis of allelic variation in genetics. J. Hered. **72**, 281–283.

Thomas, O. (1916): The grouping of the South American Muridae commonly referred to *Akodon*. Ann. Mag. Nat. Hist. (8) **18**, 336–340.

Thomas, O. (1918): On small mammals from Salta and Jujuy collected by Mr. E. Budin. Ann. Mag. Nat. Hist. (9) **1**, 186–193.

Vorontsov, N. N. (1959): Sistema khomiakov (Cricetinae) mirovoi fauny i ikh filogeneticheskie sviazi. Biuletin Moskovskogo Obshtschestva Ispitately Prirody, Otdel Biologia **44**, 134–137.

Voss, R. R.; Linzey, A. V. (1981): Comparative gross morphology of male acessory glands among Neotropical Muridae (Mammalia: Rodentia) with comments on systematic implications. Misc. Publ. Mus. Zool., Univ. Mich. **159**, 1–41.

Authors' addresses: Dr. James L. Patton and Dr. Margaret F. Smith, Museum of Vertebrate Zoology, University of California, Berkeley, CA 94720, USA, and Dr. Philip Myers, Museum of Zoology, University of Michigan, Ann Arbor, MI 48109, USA

Z. Säugetierkunde 54 (1989) 360–376

ISSN 0044-3468

Reproductive biology (behaviour, breeding, and postnatal development) in subterranean mole-rats, *Cryptomys hottentotus* (Bathyergidae)[1]

By H. Burda

Institute of Zoology, J. W. Goethe-University, Frankfurt/Main, FRG

Receipt of Ms. 7. 4. 1988

Abstract

Described for the first time breeding and reproductive biology of *Cryptomys hottentotus* in captivity. Social behaviour (greeting, hierarchy) involves features of mating behaviour. Mating and breeding in established groups were not recorded. In order to stimulate copulation and estrus, the animals were kept in pairs and re-paired daily. Gestation lasted 98 days (SD = 9, range 84–112). Next estrus after parturition was in 78 days (SD = 9). Litter size was 2 (SD = 0.7, range 1–3); male/female ratio of neonates was 1:1. Neonates weighed 7.9 g (SD = 0.5) each. They are altricial (hairless, with closed eyes), with prominent incisors, vibrissae, and partly developed physical coordination (limited active mobility, lifting head, self-scratching). Growth rate was slow: 0.36 g/day from birth to weaning and still slower afterwards. After birth of the next sibling litter, the growth rate of the juveniles of the previous litter: 1. decreased and the animals were undersized still at the age of one year if left with the family, or 2. increased and the animals were grown-up at the age of 210 days if separated from their parents. Many developmental events correlated with the attained body mass (and the age after conception?) but not with the age after birth: hair cover with mass of 10 g (SD = 1) at the postnatal age of 8–10 days; eye opening: 12.9 g (SD = 0.7), 24 (range 13–50) days; weaning: 34 g (SD = 0.3), 82 (72–105) days. Change of coat colour from black to brown to ochre was also mass dependent. Considering the body mass, *C. hottentotus* has the longest development and the lowest reproduction rate among all the rodents. This may be explained by hystricomorph affinities, subterranean life, and sociality. Reduction in activity of pregnant females and development of a caste of helpers may be understood as energy-saving mechanisms which developed in response to long pregnancy.

Introduction

Reproductive biology has been studied in representatives of most of the mammalian families, yet as far as the subterranean mammals are concerned, our knowledge of reproductive characteristics is fragmentary. These animals breed only seldom in captivity and thus the studies could not be pursued on a large scale like in other rodents or insectivores (cf. e. g. the data summarized by Eisenberg 1981 and Nowak and Paradiso 1983). As far as the endemic African family of highly specialized fossorial rodents Bathyergidae is concerned, our knowledge of reproductive biology is particularly limited. Paradoxically, most information on breeding biology has been obtained, thanks to systematic studies by Jarvis (e. g. 1969, 1978, 1979), in the naked mole-rats

[1] Dedicated to Prof. Dr. Dr. h. c. Dietrich Starck on occasion of his 80th birthday on 29. 9. 1988, and to my academic teacher, Dr. L. Sigmund, on occasion of his 55th birthday. Dr. Sigmund made me acquainted with the monumental work of Prof. Starck. They both taught me that one can hardly understand animal morphology if examining only anatomical specimens and ignoring the animals as living creatures. This paper should also commemorate the great contributions of Prof. Starck to our knowledge of subterranean mammals and his study on biology of African mole-rats published 30 years ago which became the first paper dealing with bathyergids published in Z. Säugetierkunde (1957: **22**, 50–56).

(The results were presented at the 61st Annual Meeting of the German Mammalogical Society at Berlin in 1987.)

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5406-0360 $ 02.50/0

(Heterocephalus glaber), i. e. in the most specialized and one of the least available among the bathyergids.

On the other hand, our knowledge of biology of reproduction in the most common African mole-rat *Cryptomys hottentotus* is actually next to nothing. All the ecological studies missed any convincing evidence on reproduction under natural conditions and the animals were never bred in captivity. The only observations made on captive *Cryptomys* and referring to reproductive processes are those by BATEMAN (1960) and HICKMAN (1982). BATEMAN (1960) described his unsuccessful attempt to rear a litter of three pups of unknown age but gave no clues as to the time of year when the young were found, nor as to their growth. HICKMAN's (1982) observation of copulations in mole-rats has become the first description of mating behaviour for the whole family.

To my knowledge, the present paper can be considered the first published report on birth and successful rearing of *Cryptomys* in captivity. In addition, the hitherto unknown data on the postnatal development of *C. hottentotus* from birth till the adult-like stage as well as on some other aspects of the reproductive biology and sociobiology in captivity and nature are provided.

Material and methods

A total of 41 live and freshly-dead specimens of the African common mole-rats or blesmols, *Cryptomys hottentotus* subsp. (i. e. *Cryptomys hottentotus* sensu lato, cf. KINGDON 1974), was collected in Chainda (environs of Lusaka), Zambia, between September 1984 and September 1987, sixteen of which were brought alive to Federal Republic of Germany in March 1986 and thirteen in September 1987. The animals are kept at the Institute of Zoology of the J. W. Goethe-University in Frankfurt am Main.

The animals were housed in a room with constant temperature (= 22 °C) and humidity (= 50 %) and an artificial day/night (12 h:12 h) light regime. The animals were kept in standard plastic cages for laboratory rats or glass terraria filled with horticultural peat to a depth of about 3 cm. Cage litter was changed weekly from cages inhabited by two animals. As nest material, toilet and tissue papers were provided. The animals were fed on carrots, potatoes, lettuce, and mixed grain (mostly wheat, oats, and sunflower). Occasionally apples, nuts, beet-root, sweat potatoes, black radish, and other kinds of vegetables were offered. No free water was provided.

The mole-rats from the first shipment were kept in two separate groups (12 and 4 animals) until the end of October 1986 when systematic attempts to breed them started. Four adult females (weighing 63–77 g) and four adult males (92–127 g) (captured in Oct./Nov. 1985) were selected and kept in pairs for most of the next time. Each day each female was conjointed with a different male. When the partners (or just one of them) had been reluctant to mate, or, when a series of copulations had been recorded, the animals were recombined still on the same day. Consequently each female was mated several times each day. The pairing procedure progressed until pregnancy was recognized by palpation, increase in body mass, reduced activity. Since then the pregnant females were left relatively undisturbed in a pair with a male.

Each animal was weighed each day to each third day. Except for one female and one male, the animals became fully hand-tame in the course of study. One female gave birth to one litter but was later killed by another female. Each of the remaining females bred at least twice. Altogether 18 young born in 9 litters were studies. Mean values are given with the standard deviation (SD = s_{n-1}) and/or the range (minimum to maximum found values) and the number of observations (N).

Results

Encounter, aggression

A short greeting and introducing of two unknown animals involved vocalizing; head, rump and ano-genital sniffing; pressing and rubbing chins and cheeks on one another. Usually (but not always) a fight followed between two unknown grown-up animals: 1. a larger male attacked a smaller male; 2. a smaller male (in his own cage) attacked a larger male intruder; 3. a larger female attacked a smaller female or a subadult male; 4. a female in estrus attacked other females. Fight had a character of mouth (teeth) wrestling: the animals

locked their incisors together and swayed from side to side. The males did not bite each other but tried to break (and actually broke) the incisors of the rival. Eventually the stronger male (with stronger incisors) won, the defeated male fled, showing an appeasement posture: lordosis, tail arched high, presenting posterior towards the winner, excited shaking the body, „barking". Females and subordinate males took appeasement posture even if the dominant male did not show any apparent signs of aggression. The described subordinate behaviour towards an unfamiliar male was observed as early as in a ninety-day-old male pup (and this despite the fact that the young are immune from aggression by all adults).

The fight between a male and a female lasted very long (up to one hour with short breaks) or, on the contrary, did not take place at all. Such a fight was not serious, there were no attempts to break incisors, the animals were not highly aroused, and wrestling became progressively a character of playful behaviour in which the role of the attacker frequently changed.

If a female was the attacker of another female (or a subadult male), she did not respect the appeasement postures (if any), did not try to fight mouth-to-mouth but bit the retreating animal. All the killed females were wounded in genital regions and on teats.

A male born in captivity and separated from adult animals at the age of 25 weeks (see chapter on postnatal development) attacked (when grown-up) even females, did not respect appeasement postures of defeated animals, and did not show appeasement posture when defeated himself.

Mating

The mole-rats in established groups (i. e. among the animals familiar to each other and getting along well) and in a known environment did not copulate or copulated very rarely.

Mating took place, when a male encountered: 1. a new female (in his own as well as in the female's cage), 2. a female which had been separated from the particular male for some time, 3. a female which had been soaked by a foreign smell during a contact with other animals and/or their smell (e. g. during a stay in a foreign cage).

Unfamiliar environments especially provoked mating. Thus when a pair of mole-rats had been set in a new cage, the animals copulated readily. In two cases, mating was observed even shortly after capturing the mole-rats in the field (from the same burrow system) and housing them in a cage. In another case the mole-rats copulated in a small pail into which they were put off just for few minutes while their cage was cleaned. A pair of mole-rats attempted to copulate while being transported in a small box. Mating could be repeatedly elicited in two younger animals by removal of the elder individuals from a common cage in which the group had been housed.

In general, the course of courthsip and copulation corresponded to the detailed description by Hickman (1982), so only some complementary observations will be noted here.

Although most animals vocalized intensively during courtship and copulation, some were completely silent. Many females kept on soliciting until they were eventually mated. When a male had not responed to soliciting practised by a female, he was eventually mounted by the female. Soliciting of females from males was more frequent than molesting and raping of reluctant females by males. Sometimes the female crawled during copulation carrying the male on her back. Some males attempted to grasp with teeth at the fur of the nape and shoulders of a restless female. The mounts were short (about 5 to 15 seconds). A bluish (bruised?) genital region, evident opening of the vagina, and even bleeding from the vagina were signs of estrus and/or that intromission took place.

In established and breeding pairs, even pregnant and lactating females were spontaneously (i. e. without any apparent courthsip) mounted.

Although mating was most common between appropriate sexual partners, it was

observed that a larger (dominant) animal (particularly male) mounted a smaller (subordinate) one of the same sex. Soliciting of a subordinate male from a dominant male had a typical female character but was usually only short and if the larger male did not react, soliciting ceased.

Reproductive characteristics of males

There is no scrotum in *C. hottentotus* and the testes are held abdominally. There was no behavioural evidence that the males would be seasonal breeders. I did not study morphology of the reproductive tract nor periodic changes (if any) in the size of gonads.

Estrus

Even after more than a year of living relatively undisturbed in large terraria, the animals in groups did not breed. Three weeks elapsed since the beginning of pairing experiments before the first female conceived.

Only behavioural and externally apparent symptoms of estrus were followed. The estrus in females was characterized by enhanced agility, activity, and aggressiveness against other females, intensified soliciting from adult males, a reddish and swollen genital region, drop in body mass (Fig. 1), and (as a consequence of mating?) evident opening of the vagina and bleeding from the vagina. The symptoms of estrus persisted for three to seven days.

Next conception after parturition occurred at 78.4 days (SD = 9.1; range 70–91; N = 6) and was roughly correlated with time of weaning. In two cases, when lactation (litters V and VI) was longer than the "norm", the females conceived still before weaning. If pregnancy was spontaneously interrupted (resorption of embryos, abortion), or if the litter was lost, and – in one case – after normal parturition and rearing of a single pup (litter VII), the next estrus and conception occurred within 2–3 weeks.

Gestation

Gestation lasted 98 days (SD = 9.2; range 84–112; N = 9). Pregnant females calmed down and spent most of their time in the nest. The partner males and the adolescent young supplied the pregnant females in the nest with food. The females left the nest usually only to excrete. Pregnant females put on weight regularly (Fig. 1) and increased their body mass by 20 to 35 %. The embryos could be palpated as early as about ten weeks before birth, i. e. some four weeks after conception. When held in an upright position, females in the early stages of pregnancy urinated or even defecated immediately, unable to hold back their excreta. (In animals, particularly females, not accustomed to regular handling, such an involuntary excretion occurred, however, as an apparent expression of fright.) Urine (at least initial and last drops) became progressively thick and whittish (indicating higher contents of proteins?). The whole gestation was characterized by a somewhat swollen genital region. From about the fifth week of pregnancy the inguinal teats became progressively prominent. One to two weeks before parturition, the pectoral teats (particularly the upper pair) increased in size and became more apparent, too.

Ending of several pregnancies (within first five weeks) can be explained by resorption of embryos or apparent miscarriage incidents (with bleeding from the vagina persisting for two days in one case).

One female (C3) developed a false pregnancy with all signs of a real gestation. The animal had increased its body mass and retained it since then (Fig. 1). The upper incisors became fragile. The female became aggressive and was isolated. After 15 weeks the female was joined with a male again, conceived within two weeks, and normal pregnancy followed.

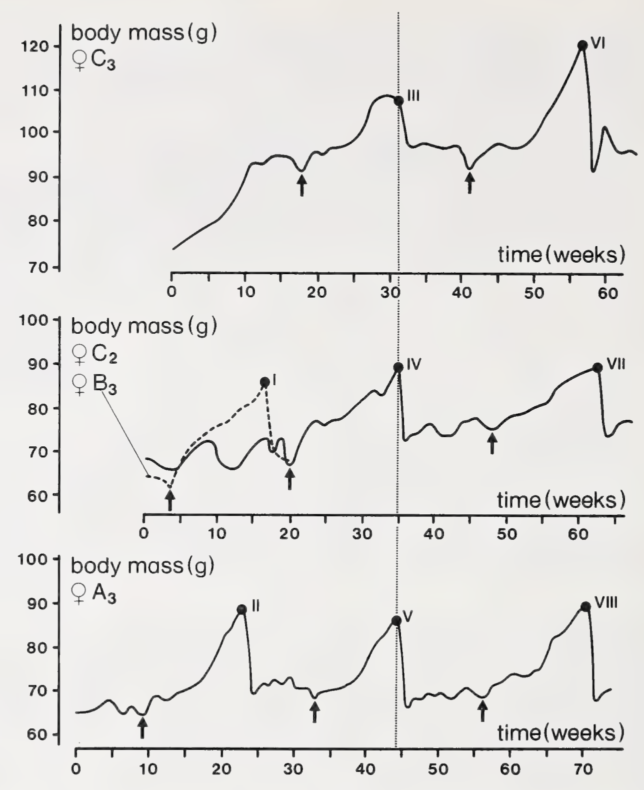


Fig. 1. Changes of body mass in four females across the time of study. 0 – start of pairing (= 27th Oct. 1986). Female B3 was killed in the 20th week by the female C2. Arrows = time of conception, Roman numerals = particular litters. The individual curves are synchronised according to one litter (intersecting vertical line)

Birth, and litter characteristics

The male and the offspring from a previous litter stay in the nest with a bearing female. The actual course of the parturition has not yet been observed. The first observations were done some 15–30 minutes after a single pup was born. The female was engaged in cleaning the neonate and herself for about one hour before falling asleep. The male "froze" in the nest and did not move at all for two hours of observation. He provided a "thermal screen" while the female put the pup between him and herself. It was noted in a litter of three that the pups must have been born in intervals of about one hour between each two pups.

The average size of a litter was 2.0 (SD = 0.75; range 1–3, N = 9). The ratio between male and female neonates was 1:1 (N = 18).

Newborn pups

Newborn pups weighed 7.9 g (SD = 0.5) (Table 1). The nose-tail tip length of the neonates was 59.9 mm (SD = 2.4) out of which 15.4 mm (SD = 1.5) was head and 5.9 mm (SD = 0.6) tail.

The neonates (Fig. 2) were practically naked, the vibrissae, however, well developed. Additionally, short tactile hairs on the body were present but still unconspicuous. Black guard hairs did not penetrate the skin yet but made it to appear rather dark in some pups.

The head spot (blaze) was apparent at birth already. The skin appeared loose, folded, and wrinkled, particularly at the neck and shoulders. The fingers, toes, and claws were normally developed. The tail appeared to be relatively longer than in grown-up animals. The incisors were prominent but not in mutual contact and were partly reddish due to the pulp showing through. The head was comparatively big and round, the snout blunt and the nose convex. A bulged skin-fold represented the auricle; the external opening of the acoustical meatus seemed to be closed. It was found out that the middle and inner ears were mature in a five-day-old pup which (apparently) did not develop after birth.

The newly born pups were able to crawl unsteadily and to hold their head lifted for few seconds.

Except for one litter (VIII) there was always an apparent dimorphic difference between the litter mates, one pup being always larger (up to 0.5 g heavier), darker, and more active.

Postnatal development

Growth

Three periods characterized by a different growth rate could be distinguished: 1. from birth to weaning, 2. weaning to birth of the next sibling litter by the mother, 3. afterwards (see Table 1 and Figs. 4, 5 for details). The growth rate was constant within the defined periods and became progressively slower in each subsequent period. In one male pup which grew slowly after birth, the growth rate increased to the norm after weaning. If left with the family in the third period, the juveniles slowed down their growth substantially and were still undersized at the age of 300 days. On the other hand, the growth rate increased in two pups which were separated from their parents (and from other adult animals) when their mother gave birth to the next litter. These animals reached the range of



Fig. 2. A three-day-old pup of *Cryptomys hottentotus*



Fig. 3. Nursing of twin 15-day-old pups

Table 1. **Body mass in neonates and growth rate in surviving pups of *Cryptomys hottentotus***

0 DAB (birth)	Pups which survived (N = 13): 8.2 (± 0.4) (range 7.9–8.8) g Pups which died (N = 5): 7.4 (± 0.2) (range 7.2–7.5) g Pups altogether (N = 18): 7.9 (± 0.5) (range 7.2–8.8) g	
0–5 DAB	Growth is constant or drops by 10 to 20 %	
5 DAB – weaning	0.36 (0.04) (range 0.26–0.42) g/day	
Weaning-birth of the next sibling litter	Females: 0.21 (0.04) (0.17–0.27)	Males: 0.31 (0.01) (0.307–0.319) g/day
Afterwards	Separated from parents Female: 0.33 g/day Male: 0.63 g/day	Left with parents Female: 0–0.08 g/day Male: 0–0.16 g/day
Age at which grown-up	210 DAB	???
DAB = days after birth		

adult-like values of body mass at about 220 days after birth (DAB) and continued to grow slowly afterwards.

Hair cover and colouration

The development of the hair coat and its colouration were primarily dependent on the attained body mass (Table 2, Fig. 4). In normally growing pups (0.32–0.42 g/day), short and thin hairs penetrated the skin 3–5 DAB. The bristle fringe on the tail and the feet was more apparent. Pups could be considered furred (with thin, still sparse but relatively long, grey hairs) after 8–10 DAB. Within few days the pelage became thick and dark slate grey to (metallic) black. Simultaneously the white hair on the blaze appeared. Later on the coat

became progressively greyish brown, brown, and eventually ochre. The animals which had been relieved of subordinance appeared to change their colour earlier. The relative size and shape of the white head spot did not change throughout the life. There was no general resemblance in the size and shape of the spot between parents and their offspring in the first filial generation.

Eyes, nose, ears, and teeth

Eye opening correlated with attaining the body mass of about 13 g at 13–50 (mostly about 23) DAB (Table 2, Figs. 4, 5).

In the course of the postnatal development, the nose flattened to become eventually adult-like, i. e. flat and somewhat concave (pig-like and slightly funnel-like) at 40 DAB.

The auricular skin-fold did not develop further. The actual opening of the external ear canal could not be recognized.

The incisors lost their reddish colouration within 1–2 DAB (5 DAB in two pups). The upper incisors grew a little quicker than the lower ones. At 3 DAB the incisors were in contact. The development of the molariform dentition was not studied.

Development of coordination

After the 5th day the (normally growing) pups tended to leave the nest spontaneously and were able to return. Frequency of leaving the nest increased each day. Self-scratching and cleaning was observed in two-day-old pups. Mutual play was recorded in the six-day-old siblings. The young tried to bite into my finger at 23 DAB. Burrowing activity and transporting of nest materials and food were observed in youngs of about 50 DAB. The pups vocalized since birth but mostly only when protesting to being retrieved or cleaned by their parents.

Feeding and parental care

The pups were suckled till attaining the body mass of about 34 g at 72 to 105 DAB (Table 2, Figs. 4, 5), when also drops of milk still could be extracted easily from the upper pair of the maternal pectoral teats. During suckling the mother was supine, and infants prone on her belly. Very rarely also huddling and sitting postures of nursing were observed. Female *C. hottentotus* have one pair of inguinal and two pairs of pectoral (the more caudal pair can be denoted axillar) teats. Only suckling from the (cranial pair of the) pectoral teats was noted (Fig. 3). In addition to being suckled, the pups began to feed on oat flakes and lettuce in 19 DAB. Attempts to feed on roots and potatoes were not successful till the age of 25 to 30 DAB. Begging for feces from an adult male (accompanied by intense vocalization) as well as autocoprophagy was observed as early as in one-month-old pups.

Both parents and even older siblings from the previous litter took care of the pups. They retrieved them into the nest whenever finding them outside. When retrieving, they grasped the body or the head of the (usually "protesting") pup between the widely opened incisors. Pups could be effectively retrieved till 25 DAB (weighing about 15 DAB). Later on the retrieval became more and more symbolical: the parents attempted to grasp the pup but apparently were not able to retrieve it because of its resistance. Eventually the retrieving attempts ceased (30 DAB, 17 g). Cleaning of pups was performed particularly by the mother. The pups preferred to sleep on bodies of their parents or between them. In families with a single pup, the parents (mostly mother) or older siblings played with the young. Play behaviour in *C. hottentotus* will be the subject of a separate report.

Table 2. **Age and body mass at which certain developmental events start to take place**

	Age (DAB)	Coeff. var. (%)	Body mass (g)	Coeff. var. (%)
Eye opening	23.6 (8.9) (13–50)	37.7	12.9 (0.7) (12.1–13.9)	5.3
Weaning	82.5 (15.4) (72–105)	18.7	34.1 (0.3) (33.8–34.5)	0.9
Apparent fur Black colour	9.3 (1.1) (8–10)	11.8	9.9 (0.9) (9.3–11.0)	9.1
Brown colour	67.0 (21.2) (51–91)	31.6	26.6 (3.8) (22.3–32.8)	14.3
Ochre colour	102.5 (14.4) (92–113)	14.4	36.4 (1.9) (35–38)	5.2

DAB = days after birth; coefficient of variation = standard deviation: mean·100. The given values are means (standard deviations and range of extreme values).

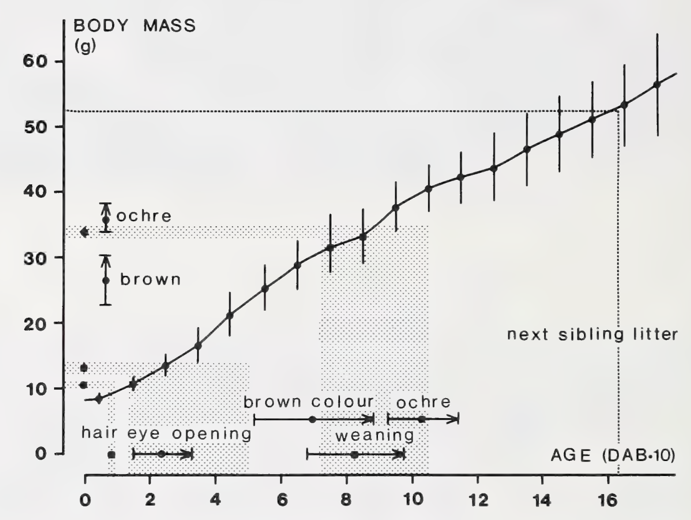


Fig. 4. Increase in body mass (mean and standard deviations) across the age (in decades of days after birth) in surviving pups. Indicated are also mean values and standard deviations of time and body mass at which certain developmental events start to appear. The horizontal and vertical strips indicate the range of extreme values for development of hair cover, eye opening, and weaning

Sexual maturity

A female born in captivity (litter II), separated from parents 160 DAB, grown-up 200 DAB und re-paired with different males each three to seven days, conceived when 340 days old but apparently resorbed the embryos a month later. Females which were not separated from the family and still remained undersized at the age of 300 days were not sexually attractive for males and were not attacked by alien females. Similarly, the undersized males did not attempt to copulate.

Mortality, infanticide

Of eighteen young born in captivity so far, five pups died within 5 to 40 DAB (killed or abandoned by their parents and/or euthanasiated because too weak to survive). They all

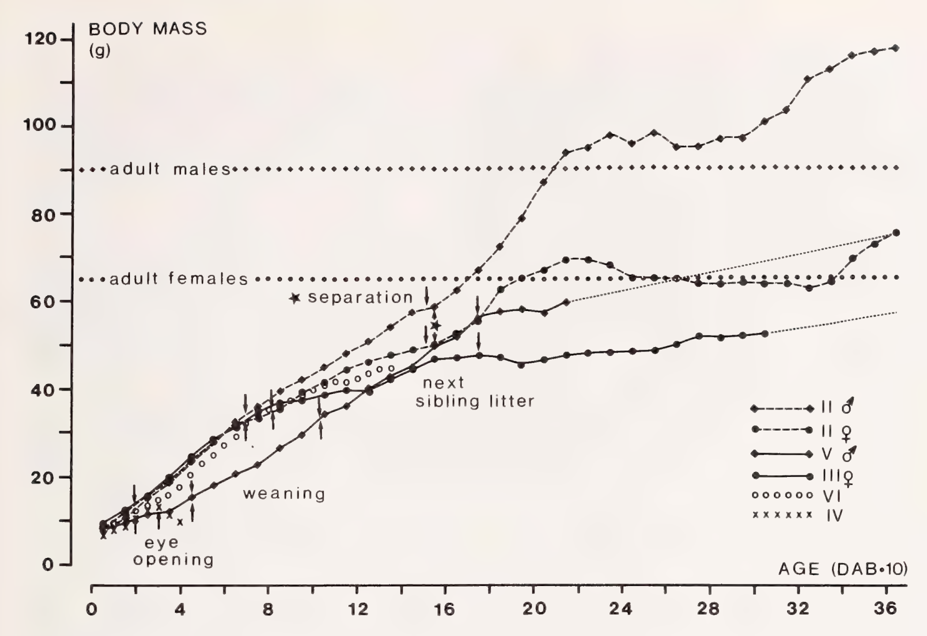


Fig. 5. Individual increase in body mass in pups of several different litters (Roman numerals). Pups of the litter II were separated, pups of the litters III and V were left with their respective families when the next sibling litter was born. Dotted lines indicate the expected trend of the further growth. Pups of the litter VI were female triplets (mean growth rate is given). Pups of the litter IV did not survive the 40th day. Adult-like values refer to lower limits of the respective ranges

were characterized by a neonate weigh less than 7.5 g. In one case, the female was found to bite off and eat the hind legs of her (still alive) five-day-old pup.

Discussion

Materials and methods

When the pairing procedure started the animals were accustomed to captivity but not to regular handling. When the females conceived for the first time, they were still aggressive. Two animals remained aggressive and yet were breeding. The pairs were living in relatively small cages with just a little soil to burrow. Some animals were kept for some time even on sand or saw dust. I kept a breeding pair at home, too. Consequently it is concluded that the defined conditions of housing, "natural housing", lack of disturbances and tameness of animals are not prerequisites for breeding *C. hottentotus* in captivity.

Encounter, aggression

The present findings indicate that appeasement posture, soliciting (and copulation) have also social function and express subordinance of an individual and thus supress aggression of a dominant male. Aggression of females (which are, in general, more aggressive than males) cannot be suppressed in this way. All recorded fatal incidents were actually caused by interacting females.

Mating

Since HICKMAN (1982) observed mating in *C. hottentotus* in an artificial burrow system into which mole-rats of two different (until then isolated) groups were introduced and since he wrote: "Copulations were effected in all regions of the tunnelways where initial encounters took place . . .", it is apparent that in HICKMAN's study the copulation was actually triggered by an encounter of two animals unknown to each other in an unknown environment as concluded in the present study.

The present findings indicate that pairings among partners from different systems may occur (as suggested also by HICKMAN 1982) and that this mating strategy may have great biological importance in reducing inbreeding. On the other hand, once a pair had been established, separated from other animals, and once it started to breed, the animals copulated repeatedly and continued to breed. Mating in (younger) animals was apparently suppressed by presence of other (older) animals.

HICKMAN (1982) compared copulatory behaviour in *C. hottentotus* to that described for subterranean myomorph rodents: *Spalax* (NEVO 1969) and geomyids (ANDERSEN 1978; SCHRAMM 1961). The differences (spontaneous nature of copulation and short intromissions in *C. hottentotus* vs. long courtship and long duration of intromissions in *Spalax* and geomyids) were explained by differences in social biology and burrow systems (social vs. solitary; copulations not restricted to particular areas vs. mating in specially constructed widened areas) (HICKMAN 1982). It is suggested here that the basic character of copulatory behaviour in *C. hottentotus* may relate to the common mating pattern exhibited by most hystricomorphs, too (cf. KLEIMAN 1974) and hence the difference may be also phylogenetic. Further comparative studies are needed to assess reflection of phylogenetic affinities and adaptive significance of copulatory behaviour.

Reproductive characteristics of males

There is no true scrotum and the testes do not descend extra-abdominally in any hystricomorph (WEIR 1974). Hence the statement by DE GRAAF (1972) that "the testes of the male *(C. hottentotus)* usually descend during the breeding season as in rats" is obscure. No hystricomorph male has been reported to be a seasonal breeder (WEIR 1974) and *C. hottentotus* is most probably not exceptional in this respect.

Estrus

The estrus (breeding) cycle in *C. hottentotus* in captivity cannot be related to the year's seasons. Nevertheless, there was periodic recurrence of estrus, once the female started to breed (cf. Fig. 1). Certain stimuli (pairing, loss of embryos or litter) elicited occurrence of estrus within three weeks. There was no postpartum estrus. Occurrence of the next estrus after parturition in *C. hottentotus* (about 78 days) is the longest cycle reported for any hystricomorph rodent (cf. WEIR 1974). The estrus can be denoted as postlactation.

Suppression of estrus and the enhanced aggressiveness of females (vs. females) was reported for *Heterocephalus*, too (JARVIS 1969).

Gestation

Occurrence of the described diagnostical symptoms of pregnancy since the estrus in which the female supposedly conceived, indicate that delayed implantation and/or embryonal diapause were not responsible for the extraordinarily long pregnancy.

A long gestation period was found in the other bathyergids too: 70 days in

Heterocephalus, at least 87 days in *Heliophobius,* and about 2–2.5 months in *Bathyergus suillus* (Jarvis 1969, 1984; the date for *Heliophobius* and *Bathyergus* are estimations).

Comparison of relative developmental times among different families of Rodentia is provided in Figure 6. In this graph, the time elapsed from conception to rearing the young of a comparable developmental level (specifically: gestation + age at which the eyes are opened and the pups are furred) was plotted against the mean adult body mass. Based on literary date (see the figure legend), mean generic values were counted and, in turn, averaged to get the "family values". The general correlation between the body mass and the length of development was described for different mammalian orders by Eisenberg (1981) and analysed in more details in Rodentia by Burda (in press). Following conclusions may be derived from the comparison provided in Figure 6: 1. Bathyergidae and some other families of Hystricomorpha have relatively long (slow) development. 2. The available data indicate that subterranean Myomorpha have an average or even shorter relative developmental length. Consequently one may speculate that the length of prenatal development is primarily determined by phylogenetic factors and the body size and that there is no general effect of the (subterranean) ecotope upon the length of gestation.

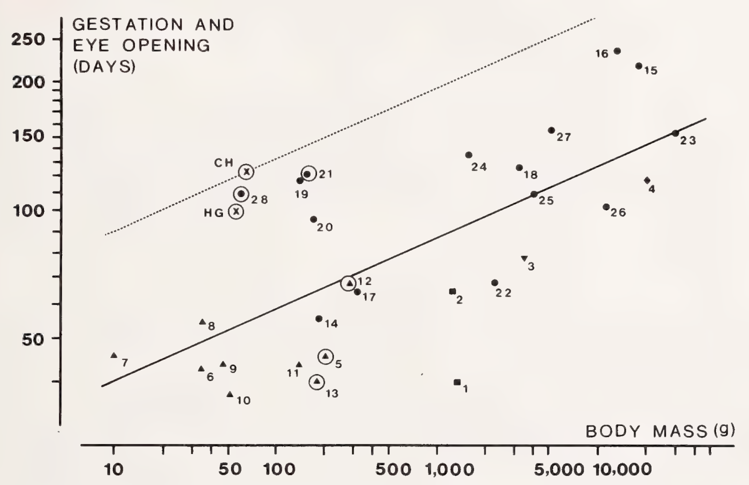


Fig. 6. Correlation between development time and mean body mass of adult females in different families of rodents. Encircled are subterranean forms. Sciuromorpha: 1 = Aplodontidae, 2 = Sciuridae; Theridomyomorpha: 3 = Pedetidae; Castorimorpha: 4 = Castoridae; Myomorpha: 5 = Geomyidae, 6 = Heteromyidae, 7 = Zapodidae, 8 = Dipodidae, 9 = Gliridae, 10 = Muridae, 11 = Cricetidae, 12 = Rhizomyidae, 13 = Spalacidae; Hystricomorpha: 14 = Ctenodactylidae, 15 = Erethizontidae, 16 = Dinomyidae, 17 = Echimyidae, 18 = Capromyidae, 19 = Abrocomidae, 20 = Octodontidae, 21 = Ctenomyidae, 22 = Caviidae, 23 = Hydrochoeridae, 24 = Chinchillidae, 25 = Dasyproctidae, 26 = Hystricidae, 27 = Thryonomidae, 28 = Bathyergidae; HG = *Heterocephalus glaber;* CH = *Cryptomys hottentotus.* Regression line (log body mass/log time): slope = 37.6, intercept = −11.8, corr. coeff. = 0.68. Based on literature data: Eisenberg (1981), Görner and Hackethal (1988), Kingdon (1974), MacDonald (1984), Walker (1975), Weir (1974), and present study

Litter size and sex ratio

Bateman (1960) reported finding of a litter of three pups, De Graaf (1972) found two females with five foetuses each; according to Smithers (1983) the number of foetuses found in *C. hottentotus* ranged from one to five. Mc Connell and Hickman (in prep., pers. comm.) found, that out of 11 *Cryptomys* females, 7 had two, 2 one, 1 three, and 1 four foetuses, which makes the mean number of foetuses to be 2.1 (SD = 0.8). No litters

were noted by Mc Connell and Hickman. My findings (mean litter size = 2.0; SD = 0.7) are thus fully consistent with the results of Mc Connell and Hickman.

A small litter size seems to be a general characteristic of bathyergids (Jarvis 1969) and hystricomorphs in general (Weir 1974). Fossorial myomorph rodents (as well as insectivores and marsupials) produce small litters, too (Nevo 1979). In particular, living in a subterranean ecotope is not strictly correlated with production of small litters. The mean litter size is twelve in *Heterocephalus* (Jarvis 1984) and five in *Ctenomys talarum* (Weir 1974), which in both cases is a relatively high offspring number for a hystricomorph rodent (cf. Weir 1974).

The sex ratio of neonates of *C. hottentotus* born in captivity was balanced between both sexes (1:1). In Zambia, we caught, however, more (subadult to adult) males than females (23:18 = 1.28, N = 41) (Burda, Kawalika, Westenberger, unpubl.). This ratio corresponds exactly to that found by Genelly (1965) (49:38 = 1.29, N = 87) in South Rhodesia (now Zimbabwe). The lower percentage of females among trapped animals in contrast to newborn pups (subjected that my sample of births in captivity is representative for wild populations of *C. hottentotus*) can be explained in two ways: 1. Higher aggressiveness in females causes sexually different mortality. 2. Females (having a long gestation and being long involved in maternal care) are less active and therefore less frequently captured than males. However, it will be postulated later on that only a small percentage of females breed.

In *Ctenomys,* the male/female ratio of alive young at birth was 1.07 (Weir 1974). The adult sex ratios (= about 0.4) in ctenomyids as well as in spalacids, rhizomyids, and geomyids are, however, unbalanced in favour of females (Nevo 1979). Since it is known that at least in *Ctenomys* and *Spalax,* the territorial aggression is higher in males than in females, it was proposed by Nevo (1979) that this factor could account for sexually differential mortality.

Newborn pups

The size of neonates was independent of sex. It was correlated with the length of gestation (which was variable!) partly combined with the litter size. The litter size as a sole factor was not however, informative of the body size. Body mass of neonates amounted to about 11 % of the maternal weight. In general, relatively large neonates are typical for most hystricomorphs (Weir 1974). In contrast to most other hystricomorphs, the *Cryptomys* neonates should not be called precocious at all. There is some resemblance to the neonates of ctenomyids and octodontids (cf. description provided by Weir 1974) but the altricial state of *Cryptomys* neonates is still more pronounced and persists for a longer time. Similarly, *Heterocephalus* and *Heliophobius* are born at an altricial level (Jarvis 1969). It is reasoned elsewhere (Burda in press) that altriciality in *Octodon – Ctenomys – Cryptomys – Heterocephalus* is a consequence of reducing the body size in these genera of hystricomorph rodents. Yet compared to e. g. the house mouse or to laboratory rats, the *Cryptomys* neonates are psychophysically more developed.

Postnatal development

The long postnatal development seems to be a general characteristic for the family Bathyergidae. According to Jarvis (1978) it may take a juvenile *Heterocephalus* at least a year to reach adult size.

It is highly probable that the growth rate (at least after the age of about six months) is under a pheromone control of adult animals. Pheromonal effect upon the acceleration or retardation of growth and/or puberty is known or suspected in *Heterocephalus* (Jarvis 1984), some other hystricomorph rodents (Rowlands and Weir 1974), and in rodents in general (Brown 1985).

The rate of postnatal growth did not correlate with sex, nor with the number of litter mates. However, the pups which were relatively undersized at birth continued to grow slowly or did not grow at all and eventually died. Due to individual differences in the rate of postnatal growth, it may be concluded that certain aspects of physical and psychical development (particularly eye opening, development of hair cover and its colouration, leaving the nest) and weaning depended primarily on the attained body size and not on the actual age.

The statement in Nowak and Paradiso (1983) that "even the newborn (bathyergids) can inflict severe bites" seems to be exaggarated – at least if presented as it is, i. e. as a family characteristic. The statement by De Graaf (1972) that "the females often start breeding before reaching maturity" seems to be unwarranted as well.

Coat colour

The colour change of the pelage is another interesting phenomenon and will be subject of a more detailed report (in prep.). Coat colour in *Cryptomys* was treated as a taxonomical or ecological feature related to geographic distribution and/or to soil colour (cf. Ansell 1960; De Graaf 1972; Rosevear 1969). While in *Spalax,* the coat colour was found to vary with the substrate and thus to be adaptive (Nevo 1979; Heth et al. 1988), a lack of a selective factor for coat colour in *Cryptomys* was suggested (Genelly 1965). Poduschka and Nopp (1978) found their *C. hottentotus* to change their individual colour after coming to captivity. The authors attributed the phenomenon to the change of soil conditions. De Graaf (1972) and Genelly (1965) concluded that the coat colour was independent of age. Smithers (1983) writes correctly that the juveniles tend to be darker than adults but does not give any further details.

As found in the present study, each animal in the course of its individual life changed its colour markedly several times. This change was independent of substrate and of sex. The change followed the same trend in all the studied animals. Timing of changes was correlated with the attained body mass and thus with age and social status.

Parental care, interactions between parents and offspring

The position adopted by the young during suckling and the mother's nursing posture in *Cryptomys,* i. e. mother supine and infants prone, was not reported for any other (hystricomorph) rodent (cf. Kleiman 1974).

So far, there have not been any indications that the adolescent and grown-up mole-rats would be repulsed by their parents. On the contrary, they were fully integrated into the group life. I can confirm the observation by Roberts (cited by Kingdon 1974) that the younger animals were usually the first to be trapped. Robert's explanation that "this suggests that the older animals drive out the younger ones to forage and bring back food to the storage chamber" is, however, speculative. A more plausible explanation was presented by Hickman (1980): the young animals are inexperienced, more explorative and less cautious. In addition, I observed young animals to be more active and spending more time outside the nest than older animals. Yet when isolated, there was no difference in activity patterns between different age (weight) groups (Hickman 1980).

Breeding cycle in captivity and in nature

The period between two subsequent births given by a particular female was 25.2 ($\pm$2.2) (range 22–27) weeks. It can be concluded that (at least in captivity) the female *C. hottentotus* may (successfully) breed twice a year.

Most of the hystricomorph rodents (Weir 1974) and most of the fossorial mammals

(NEVO 1979) are known to have long breeding cycles. *Heterocephalus glaber* is an exception since a female may produce a large litter every 80 days. Offspring production is, however, efficiently minimized in other ways (JARVIS 1984).

Practically nothing is known on the breeding cycle of *C. hottentotus* in nature. The available samples are too small and not comparable. *C. hottentotus* is considered to be a seasonal breeder probably breeding once a year (GENELLY 1965; KINGDON 1974; JARVIS 1984), or it is supposed to breed throughout the year (ANSELL 1960; SMITHERS 1983).

Subjected that growth rate in nature is comparable to that found in captivity, date of birth can be estimated in juveniles weighing less than 45 g (and younger than 6 months). Of 41 mole-rats captured in Zambia from July to December during two subsequent years (BURDA, KAWALIKA, WESTENBERGER) only six animals could be divided into three distinct age groups: animals born in February/March (N = 4), May (N = 1), August/September (N = 1). (The youngest pup must have been only 40 days old.) These findings indicate that there is no clear relation between the timing of breeding seasons and climatic regime for *C. hottentotus* in Zambia.

Many observations (referring to pairing behaviour, interactions between adult animals, between parents and offspring, between offspring from different sibling litters) made in captive animals and described in this study, allow speculations that the natural groups inhabiting particular burrow systems are families consisting of a single breeding parental pair and its offsprings from different litters. In other words: it is suggested that there may be many adult females and males which do not breed. An analogous (but probably still more pronounced) situation is known in *Heterocephalus glaber* (JARVIS 1972, 1984). The "helpers" in *Cryptomys* families are smaller and darker (more brown, less ochre) than the breeding pair.

Since *C. hottentotus* and *Heterocephalus glaber* are the smallest forms among all hystricognath rodents and thus are characterized by relatively and absolutely long developmental times, respectively (see also BURDA in press), strategies to reduce energy budget had to be developed. The overall reduced activity of the female during pregnancy as well as development of (eu)sociality and establishment of the caste of helpers may be understood as such strategies. These reasonings may explain why only so few findings of pregnant females were recorded in the literature.

Conclusions

K-strategy was adopted (as a phylogenetic trait) by most of the hystricomorphs (WEIR 1974), and (as an adaptive convergent trait) by most of the subterranean mammals (NEVO 1979) and by many mammals forming complex social groups (EISENBERG 1981). *C. hottentotus* being a socially living subterranean hystricomorph combines all the three prerequisites for K-strategy. Actually all the factors reducing reproduction rate are present in *C. hottentotus*: long prenatal and postnatal development, small litter size, no postpartum estrus (?) and thus at a maximum two breeding periods possible across the year (?), a long time spent by pups in learning situation, and selection for a temporary non-reproductive caste. Combination of all these factors make the K-strategy in *C. hottentotus* most effective (and the reproduction rate relatively slowest) among all the rodents. In many aspects of its reproductive and social biology, *C. hottentotus* seems to resemble *Heterocephalus* (cf. papers by JARVIS). It is suggested that this similarity is primarily due to hystricomorph (hystricognath) affinities and small body size. The abiotic and biotic factors characterizing their respective habitats are, however, different in both species.

Acknowledgements

The animals were collected during my senior lecturership at the University of Zambia (1984–1986), and this would not have been done if it were not for my student, Mr. Mathias Kawalika, whose great and devoted assistance in the field is highly appreciated. The study on captive animals would not be conducted if it were not for Prof. Dr. V. Bruns (Frankfurt/M) who provided generously refuge for me and my animals in his laboratory. Stimulating discussions were held with Dr. D. Kock (Frankfurt) and Doz. Dr. W. Poduschka (Wien) who supplied me with literature. Most valuable comments and advice to the first draft of the manuscript were provided by Prof. Dr. G. C. Hickman (Pietermaritzburg), Prof. Dr. E. Nevo (Haifa), Doz. Dr. W. Poduschka, and Prof. Dr. P. Vogel (Lausanne). Prof. Dr. G. C. Hickman and Doz. Dr. W. Poduschka helped to improve the manuscript through their linguistic corrections and suggestions. Last but not least my great thanks are due to Mrs. Gabriele Elter, my wife Jana, and Dr. J. Novotny (Lusaka) for their devoted and enthusiastic assistance.

The study was supported by the Alexander von Humboldt-Foundation and Deutsche Forschungsgemeinschaft (SFB 45/B 21).

Zusammenfassung

Fortpflanzungsbiologie (Verhalten, Zucht und postnatale Entwicklung) subterraner Graumulle, Cryptomys hottentotus (Bathyergidae)

Es wird erstmalig über die regelmäßige Aufzucht von *Cryptomys hottentotus* in Gefangenschaft berichtet, und die wichtigsten Aspekte der Fortpflanzungsbiologie werden beschrieben. In einer geordneten Gruppe und in bekannter Umwelt wurden keine Kopulationen beobachtet. Um die Tiere zur Paarung zu stimulieren, wurden sie in Paaren gehalten, und die Paare wurden täglich neu kombiniert. Die Tragzeit betrug 98 Tage (Standardabweichung 9, Min. 84, Max. 112 Tage). Der nächste Östrus mit Konzeption war nach 78 (S. A. 9) Tagen. Die Wurfgröße betrug 2.0 (0.75, 1–3). Das Verhältnis zwischen weiblichen und männlichen Neugeborenen lag bei 1:1. Das Geburtsgewicht betrug 7.9 g (S. A. 0.5). Die Neugeborenen sind nackt, haben geschlossene Augen, besitzen jedoch entwickelte Schneidezähne und Tasthaare. Selbstkratzen, unbeholfene Lokomotion und Kopfheben wurden bereits ein bis zwei Tage nach der Geburt beobachtet. Das Wachstum war langsam: 0.36 g/Tag bis zum Absetzen und danach noch langsamer. Nach der Geburt des nächsten Geschwisterwurfes wurde das Wachstum der Jungen aus dem ersten Wurf: 1. stark vermindert, und die Jungtiere waren im Alter von einem Jahr noch nicht erwachsen, wenn sie bei der Familie blieben; oder 2. stark beschleunigt, und die Tiere waren im Alter von 210 Tagen erwachsen, wenn sie von den Eltern getrennt waren. Wichtige Entwicklungsereignisse und die Fellfarbenänderung (von schwarz zu braun zu ocker) waren mehr vom erreichten Körpergewicht bzw. vom Alter nach der Konzeption, jedoch nicht vom Alter nach der Geburt abhängig: So war die Behaarung beim Gewicht von 10 (S. A. 1) g im Alter von 8–10 Tagen vollständig; Öffnen der Augen: 12,9 (S. A. 0.7) g, 24 (13–50) Tage; Absetzen: 34 (S. A. 0.3) g, 82 (72–105) Tage. Unter Berücksichtigung der Körpergröße hat *C. hottentotus* unter allen Nagetieren die relativ langsamste Entwicklungsgeschwindigkeit und die relativ geringste Fortpflanzungsrate. Dieses kann auf die hystricomorphe Verwandtschaft, subterrane Lebensweise und die komplexe Sozialstruktur dieser Art zurückgeführt werden.

References

Andersen, D. C. (1978): Observations on reproduction, growth, and behavior of the northern pocket gopher *(Thomomys talpoides)*. J. Mammalogy **59**, 418–422.

Ansell, W. F. H. (1960): Mammals of Northern Rhodesia. Lusaka: Govt. Press.

Bateman, J. A. (1960): Observations on young mole rats. African Wild Life **14**, 227–234.

Brown, R. E. (1985): The rodents I: effects of odours on reproductive physiology (primer effects). In: Social odours in mammals. 1. ed. Ed. by R. E. Brown and D. W. MacDonald. Oxdford: Clarendon Press. 245–344.

Burda, H. (in press): Relationships among rodent taxa as indicated by characteristics of reproductive biology. Z. zool. Syst. u. Evolut.-forsch.

De Graaf, G. (1972): On the mole-rat (*Cryptomys hottentotus damarensis* [Rodentia]) in the Kalahari Gemsbok National Park. Koedoe, Pretoria, **15**, 25–35.

Eisenberg, J. F. (1981): The mammalian radiations. London: The Anthlone Press.

Genelly, R. E. (1965): Ecology of the common mole-rat *(Cryptomys hottentotus)* in Rhodesia. J. Mammalogy **46**, 674–665.

Görner, M.; Hackethal, H. (1988): Säugetiere Europas. München: Deutscher Taschenbuch Verlag.

Heth, G.; Beiles, A.; Nevo, E. (1988): Adaptive variation of pelage color within and between species of the subterranean mole rat *(Spalax ehrenbergi)* in Israel. Oecologia **74**, 617–622.

Hickman, G. C. (1980): Locomotory activity of captive *Cryptomys hottentotus,* (Mammalia: Bathyergidae), a fossorial rodent. J. Zool., Lond., **192,** 225–235.
— (1982): Copulation of *Cryptomys hottentotus* (Bathyergidae), a fossorial rodent. Mammalia **46,** 293–298.
Jarvis, J. U. M. (1969): The breeding season and litter size of African mole-rats. J. Reprod. Fert., Suppl. **6,** 237–248.
— (1978) Energetics of survival in *Heterocephalus glaber* (Rüppel), the naked mole-rat (Rodentia, Bathyergidae). Bull. Carnegie Mus. Natl. Hist. **6,** 81–87.
— (1979): Ecological studies on *Heterocephalus glaber,* the naked mole-rat, in Kenya. Natl. Geogr. Res. Reports, 429–437.
— (1984): African mole-rats. In: The encyclopaedia of mammals 2. ed. Ed. by D. MacDonald. London–Sydney: George Allen and Unwin. 708–711.
Kingdon, J. (1974): East African Mammals. 2/B. London–New York: Academic Press.
Kleiman, D. G. (1974): Patterns of behaviour in hystricomorph rodents. Symp. zool. Soc. Lond. **34,** 171–209.
MacDonald, D. (Ed.) (1984): The encyclopaedia of mammals: 2. London–Sydney: George Allen and Unwin. 594–711.
Nevo, E. (1969): Mole rat *Spalax ehrenbergi:* mating behavior and its evolutionary significance. Science **163,** 484–486.
— (1979): Adaptive convergence and divergence of subterranean mammals. Ann. Rev. Ecol. Syst. **10,** 269–308.
Nowak, R. M.; Paradiso, J. L. (1983): Walker's mammals of the world. 4th ed. Baltimore–London: The Johns Hopkins Univ. Press.
Poduschka, W.; Nopp, H. (1978): Fellfarbenänderung gefangengehaltener Mullratten, *Cryptomys hottentotus* (Lesson, 1826). Säugetierk. Mitt. **26,** 275–279.
Rosevear, D. R. (1969): The rodents of West Africa. Trustees of the British Museum. 551–565.
Rowlands, I. W.; Weir, B. J. (Eds.) (1974): The biology of hystricomorph rodents. Symp. zool. Soc. Lond. **34,** 171–209.
Schramm, P. (1961): Copulation and gestation in the pocket gopher. J. Mammalogy **42,** 167–170.
Smithers, R. H. N. (1983): The mammals of Southern African subregion. Pretoria: Univ. of Pretoria Press, 177–185.
Walker, E. P. (1975): Mammals of the world. 3rd ed. Baltimore–London: The John Hopkins Univ. Press.
Weir, B. J. (1974): Reproductive characteristics of hystricomorph rodents. Symp. zool. Soc. Lond. **34,** 265–301.

Author's address: Dr. Hynek Burda, Institute of Zoology, Johann-Wolfgang-Goethe-University, Siesmayerstr. 70, D-6000 Frankfurt am Main 11, FRG

Z. Säugetierkunde 54 (1989) 377–392

ISSN 0044-3468

Foraging in polecats (*Mustela putorius* L.) of Switzerland: The case of a specialist anuran predator

By. D. Weber

From the Museum of Natural History, Basel, Switzerland

Receipt of Ms. 15. 3. 1988

Abstract

Studied the foraging behaviour of 12 radio-tracked polecats (*Mustela putorius* L.) in a mountainous and a lowland area of Switzerland and of captive-held animals. Five different foraging options are described, of which at least three are self-excluding: 1. Hunting small mammals in and around houses; 2. Hunting rats in rubbish dumps; 3. Collecting anurans in suitable forests; 4. Collecting eggs, pet food or offal in and around houses; 5. Collecting offal in rubbish dumps. Mammals are easily found by polecats, but are difficult to seize. Anurans are difficult to find but easy to seize. Frog-collecting polecats seek intensively in one small area for one or more foraging bouts, and then leave for another, somtimes distant area. The resulting pattern can best be described as nomadic; a polecat may not return to a given area for some weeks or months.

It is hypothized that Swiss polecats are specialized anuran foragers because they are awkward rodent hunters. There are two reasons for taking other foraging options: 1. extreme local concentrations of food (e.g. rubbish dumps, carcasses, hen houses), and 2. extreme travelling costs between resting sites and amphibian-hunting areas (in winter, when polecats are forced to rest inside houses).

Introduction

Polecats are usually described as relatively unspecialized carnivores (e.g. Tschudi 1858; Brehm 1879; Grashey 1894; Hainard 1948; Herter 1959; Rahm 1976; Walton 1977). Some of these authors also mention a certain preference for fruits or honey. Food analyses from all over Europe confirm this (Goethe 1939; Kratochvil 1952; Danilov and Rusakov 1969; Rzebikkowalska 1972; Brugge 1977; Mermod et al. 1983). Recent investigations on the diet of polecats from Switzerland have revealed a dominance of anurans (Weber 1988a). This was already mentioned by Rohrdorf (1853) and agrees with observations of Labhardt (1980).

Prey-catching and related behaviour in polecats and ferrets has been intensively studied under laboratory conditions (Goethe 1940; Räber 1944; Herter 1953; Eibl-Eibesfeldt 1956; Wüstehube 1960; Gossow 1970; Apfelbach 1973; Apfelbach and Ebel 1975; Appelbach and Wester 1977). In contrast, we know almost nothing of the foraging behaviour of wild polecats. Herrenschmidt (1982) and Nilsson (1978) radio-tracked some individuals, but did not investigate the feeding habits of these animals.

The present study attempts to close this gap, in describing the foraging behaviour of the only specialized predator of anurans among the mammals of central Europe.

Material and methods

The lowland study area

The "Leimental" is a lowland valley on the Franco-Swiss border south-west of Basle (47° 30′ N, 7° 29′ E; altitude 300–450 m). Compared to the rest of Switzerland, the climate is mild with warm winters (January mean 0 °C). The vegetation period is approximately 210 days. Snow-cover occurs only on few days of the year, most often in February.

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5406-0377 $ 02.50/0

The dominating land use of the Leimental is arable farming. The main structuring elements of the countryside are strips of woodland along brooks. Between the fields there are locally a few drainage ditches, which in summer are overgrown by shrubs. The hilltops are mostly covered with patchy and irregular-shaped forests of various areas, crossed by many small brooks. These forests consist of old oak, beech and other deciduous trees with local occurrence of conifers (mainly old plantations of silver fir). Clear-cuttings are small, and often left to natural succession. Where the canopy is thin, the ground is covered with large thickets, dominated by bramble.

Farmhouses are mostly concentrated in the villages. Near Basle the rural character of the valley changes to a suburban one, with industrial areas, densely built-up centres and large areas with houses and gardens.

The mountain study area

The mountains of La Brévine (46° 58′ N, 6° 39′ E; altitude 1000–1300 m) are a chain of the Swiss Jura mountains south of the village of La Brévine. For the geographical latitude, the climate is cold with harsh and long winters and a vegetation period of about 140 days (January mean –4 °C, annual mean +4 °C). Temperatures below –30 °C occur regularly.

About half the area is covered with mountain forests, with spruce, fir and sycamore as dominant tree species. Locally, there are almost pure stands of spruce to be found. Forestry operates without clear-cutting; only selected individual trees are cut, and there are no plantations. This results in richly-structured stands on a small scale and in a highly uniform appearance of the woodlands on a large scale. The forest's floor is densely covered with shrubs, bushes, young trees and dead branches.

The rest of the area is mainly covered by grassland and wooded pastures, which are divided by stone walls, hedges, and combinations of both. Farmhouses and stables are isolated and scattered; not all of them are used in winter. There is almost no surface water in this study area.

Methods

Polecats were captured in wooden box traps (85 × 16 × 24 cm) baited with mice or tinned sardines. Captured specimens were sedated with an intramuscular injection of 20 mg Vetalar® (Parke, Davis and Co, Detroit, USA) and equipped with a collar containing a transmitter (type MV/A, Karl Wagener, Cologne, West Germany). The weight of the radio collars was about 30 g, transmitting frequencies around 148 mHz. A female reared in captivity was also radio-tracked after her release. Systematic observations of this individual started 5 weeks after her release. During this period, she had mated, and her behaviour showed no obvious differences to that of wild individuals. All radio-tracked polecats were adults (Table 1).

Table 1. **Radio-tracked polecats, study areas and observation periods**

Identification (name)	Sex	Study area	Start of observation	Last observation
Viva	f	Leimental	15. 9. 83	17. 9. 83
Dickkopf	m	Leimental	22. 12. 83	12. 6. 84
Phlegma	m	Leimental	2. 3. 84	16. 3. 84
Methusalem	m	Leimental	27. 3. 84	11. 4. 84
Schaggeli	f	Leimental	27. 4. 84	14. 7. 84
Mülla	f	Leimental	24. 7. 84	23. 8. 84
Micro	f	Leimental	3. 9. 84	27. 10. 84
Urs	m	Leimental	21. 10. 84	25. 11. 84
Jean-Marc	m	La Brévine mountains	1. 6. 84	18. 8. 84
Claude	m	La Brévine mountains	12. 2. 85	27. 2. 85
Paul	m	La Brévine mountains	12. 2. 85	16. 4. 85
Philippe	m	La Brévine mountains	14. 4. 85	3. 5. 85

The animals were located with a receiver and a hand-held H-type aerial (Karl Wagener, Cologne, West Germany). The constancy of signal strength showed whether an animal was resting or moving. Two types of observation were made: 1. During daytime I located the sites of resting polecats and searched there for scats and prey remains. I recorded location (50 m coordinate grid), date, time, weather and the type of resting place. 2. Periodical monitoring of individuals for (normally) 6 hours was performed by following animals on foot, at close distance. Every 10 minutes, coordinates (50 m grid), habitat, weather, activity of the animal and special observations were recorded. In the Leimental area, distances to active polecats could usually be kept at about 50 m or less; in the La Brévine

mountains, due to the difficult topographical situation or to snow-cover, distances were often greater. The animals often made so much noise while moving around that I was able to follow them simply by listening. Monitoring usually took place at night, during the period of highest activity (WEBER 1987).

The habitat types available to individual polecats were quantified by means of 50 m or 100 m gridpoints, which were laid over the minimum-convex-polygon (TREVOR-DEUTSCH and HACKETT 1980) of all locations of the individual concerned.

Techniques of scat analyses and quantitative treatment of these findings are given elsewhere (WEBER 1988a). Results are calculated as weighted relative frequencies of occurrence. Note that prey remains of less than an estimated 25 % of scat volume have been disregarded.

Some direct observations and experiments regarding hunting behaviour were made in an enclosure of 200 m^2, with two hand-reared, adult male polecats. Experiments to investigate hunting success in relation to prey species and vegetation cover were made in a 2 × 2 m cage within the enclosure. Polecats were trained to expect prey in this cage and to hunt it there. They could enter and leave this cage at will. The prey animals were not able to escape from this smaller cage.

The hunting experiments were performed in the following manner: A prey animal was placed in the hunting cage. Then, presumably attracted by scent, a polecat would enter the cage and attempt to catch the prey. Based on definitions of GOSSOW (1970), I protocolled on a tape-recorder the following phenomena: 1. The beginning of the searching phase, which is marked by signs of positive exitement, hasty, undirected movements and sniffing around on the ground; 2. The moment of attack (raised head, jumping instead of walking, visual or acoustical orientation); 3. The end of the attack (either grasping the prey, or beginning another searching phase, if the prey has escapted by jumping away or by immobility); 4. The success of the attack; 5. The number of grasping attempts during the attack; 6. Special events depending on situations. Later, the durations of searching phases and attacks were timed with a stopwatch while playing the protocol tapes. Details of these experiments and their results are given elsewhere (WEBER 1987). Here, only successes of attacks are reported (successful = grasping the prey; unsuccessful = attack without grasping, followed by a new searching phase).

Results

Hunting techniques

Direct observations of wild polecats catching prey were rare. This was mainly due to the strong connection of polecats with dense vegetation: Even at distances of 2 or 3 metres I could not normally see foraging polecats. In some cases, information on hunting techniques resulted from tracks. Therefore, most results presented in this chapter stem from experiments with the two captive polecats, to which I fed more than a dozen anurans and over 100 small rodents of different species (WEBER 1987). Additionally, some experiments with dead prey were performed.

The smell of mice or voles stimulated the captive polecats to excited searching behaviour at distances of about five metres and more. Dead mice thrown into the enclosure were normally found after several minutes of undirected searching. The polecats sometimes rummaged only a few centimeters from the prey without detecting it. Prey finding was greatly eased by pulling the dead mice some metres over the ground with a kind of fishing rod (to produce a scent track): When they first crossed the track while searching, they immediately stopped and followed the scent, keeping the nose to the ground, until they reached the mouse. They hereby often followed a trace in the wrong direction until the starting point, and had to turn back. Living rodents presented in the experimental cage where found in the same way.

Compared to natural conditions, mice and voles in the 4 m^2 experimental cage were handicapped in avoiding polecat attacks: They were confronted with an unfamiliar environment with no sure escape routes (e.g. holes, trees). However, they often successfully escaped from polecats approaching on their track by jumping away *(Apodemus)*, or by remaining motionless until the polecat had run over them *(Apodemus, Clethrionomys)*. Especially in dense vegetation structure, polecats showed a high rate of unsuccessful attacks on rodents (Table 2). A wild polecat was observed catching a vole *(Microtus agretis)* by "ploughing" with its muzzle along the vole's tunnel.

I never observed any reaction by polecats to the presence of immobile anurans nearby.

Table 2. **Rodent-hunting success of 2 polecats under experimental conditions (2 × 2 m cage)**

	Only leaf-litter on ground			Cage structured with heap of twigs		
	N_a	N_s	% S	N_a	N_s	% S
Apodemus	128	84	65.6	88	36	40.9
Clethrionomys	17	17	100.0	17	12	70.6

N_a is the total number of attacks, N_s the number of successful attacks (ending with grasping the prey) and % S is the proportion of successful attacks (percent). Different hunting successes are significant ($p < 0.001$ for *Apodemus;* $p < 0.02$ die *Clethrionomys;* χ^2-tests). Note that there were no holes or other protected places for the rodents in the experimental cage

There was no sign of stimulation by odour or scent tracks. Frogs were found by chance while the polecat was searching at suitable places. To provoke attacks, immobile frogs had to be touched with the nose, the mouth or the vibrissae. When polecats approached, frogs *(Rana temporaria)* and toads *(Bufo bufo)* often avoided detection by pressing themselves to the ground. I never saw an attacked anuran attempt to jump away; once detected, they were always caught.

In winter, polecats also eat anurans when these are hibernating underground. Several times, I found places where polecats had dug up frogs or toads during winter. Such holes were normally not deeper than about 30 cm. I never made an observation that gave me any idea of how polecats are able to detect hibernating anurans. Surprisingly, they found them even in frozen soil and under snowcover of more than a metre.

I once observed an encounter between a radio-tracked female polecat and a hedgehog *(Erinaceus europaeus).* She sniffed with excitement at the rolled-up animal, but made no attempt to bite it. After a few minutes, she lost all interest and continued rummaging around for other prey. Remains of small birds found on polecat snow-tracks never showed blood. I therefore assume that the birds had been found aready dead and frozen.

The polecats regularly found eggs in barns and stables where poultry was allowed to range freely during daytime. Often the farmers did not know that eggs had been taken, as the polecats found only those eggs which had been missed by the farmers in the evening. I never observed attacks on chickens, even when these were sleeping in the same barn as the polecat. The ability of polecats to enter hen-houses was poor; they only succeeded when there was an entrance at ground-level.

I once observed a male polecat who tried to enter a poultry yard, for 30 minutes without success, until he was chased away by some geese. The same individual was able to steal eggs from brooding turkeys during the night.

The polecats always took their prey to a hidden and undisturbed place before feeding. The captive polecats in the enclosure could be prevented from feeding by continuous offers of food; they did not start feeding, as long as there was still food to be hidden. When they knew each other's food-hiding, they often performed long reciprocal stealing behaviour before starting to feed.

Sometimes, polecats catch and hide more food than they will eat afterwards. Following radio-tagged animals, I found nine heaps of anurans (which had only partly been eaten) in different numbers near polecat hiding-places. Some had not been eaten, but only killed or injured by bites in the head or neck.

The largest heap was one of 16 common frogs *(R. temporaria)*, of which some were still alive. When there are sufficient anurans available, polecats eat only the leg muscles (Fig. 1). In other cases, even toads were eaten entirely, which was also indicated by the regular occurrence of cranial bones in polecat scats.

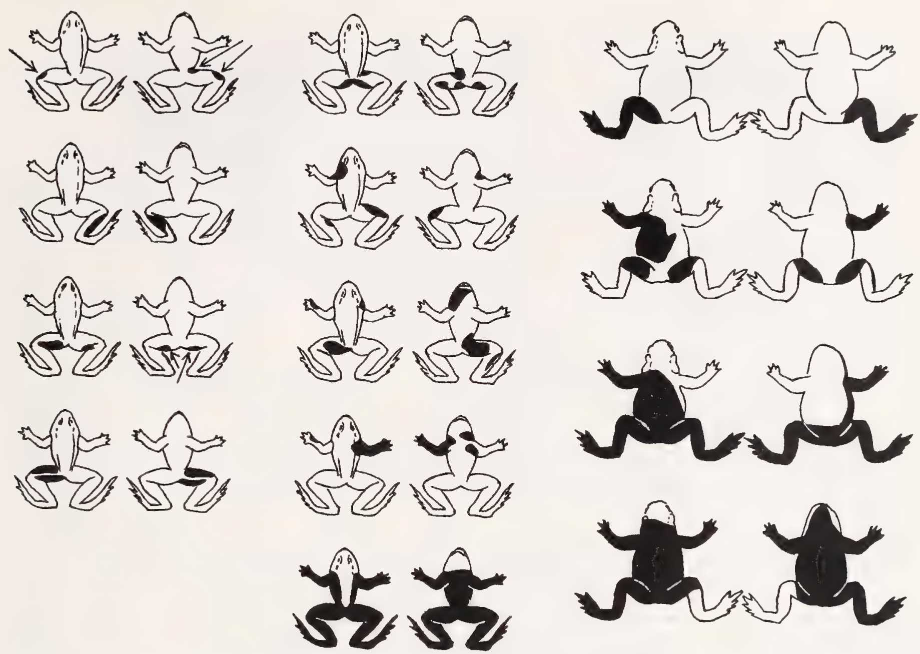


Fig. 1. Anurans killed by polecats but not completely eaten. Common frogs *Rana temporaria* and common toads *Bufo bufo*. Parts eaten in black. View from above *(left)* and below *(right)* on the same individuals

Hunting grounds

Table 3 shows all records of active polecats in different habitat types (pooled data from single daytime observations and 10-minute-interval localisations during consecutive monitoring). Forest, farmhouses and refuse dumps make up nearly 90 % of the records, and can be considered as typical polecat habitats. Within the agricultural land category, polecat presence was nearly always restricted to special structures between fields and meadows. Some of the farmhouses used by polecats were situated in the centres of large villages. Records from gardens originate mainly from places near forests. The category "forest" was not subdivided for this analysis, as it was often impossible to attribute a localisation to one of the different forest types available; often, the patches were too small and the localisations not precise enough. According to my subjective impression, the most attractive forest stands were shrubby thickets, and the least attractive those with bare ground below the canopy.

All individuals with such areas within their ranges avoided agricultural areas (Table 4). Rubbish dumps were a rare but attractive resource in the Leimental study area. The three polecats which had dumps within their range spent 83 % (Micro), 40 % (Phlegma) and 19 % (Urs) of their recorded activity at these places.

Forests and houses were within the range of every animal. In the lowland study area, houses were mainly used during winter and spring, whereas in the mountain area, the polecats were mostly active in forests during these seasons also (Fig. 2).

The bulk of food passes through the polecat gut within a few hours (Goethe 1940), which allows prey remains in fresh scats to be attributed to the foraging of the previous night. Within a single foraging bout, the polecats usually concentrated their activities on one of the three habitat categories forest, buildings and dumps: In 112 of 133 activity bouts, they were recorded to more than 80 % within only one of these three habitats.

Table 3. **Records of active polecats in different biotopes**

Biotope	Leimental N	Leimental %	La Brévine mountains N	La Brévine mountains %	Total N	Total %
Woodland	*572*	*56.5*	*329*	*80.4*	*901*	*63.4*
Agricultural land	*67*	*6.6*	*49*	*12.0*	*116*	*8.2*
hereof: fields	7	0.7	0	0	7	0.5
grassland	8	0.8	3	0.7	11	0.8
wooded pastures	0	0	18	4.4	18	1.3
marsh, bank	6	0.6	0	0	6	0.4
fallow grounds	23	2.3	0	0	23	1.6
hedges, ditches	23	2.3	28	6.9	51	3.6
Settlements, houses	*197*	*19.4*	*31*	*7.6*	*228*	*16.0*
hereof: farms, vegetable gardens	164	16.2	31	7.6	195	13.7
gardens	28	2.8	0	0	28	2.0
centre of town or village	3	0.3	0	0	3	0.2
industrial area	2	0.2	0	0	2	0.1
Rubish dumps	*177*	*17.5*	*0*	*0*	*177*	*12.4*
Total	1013	100.0	409	100.0	1422	100.0

Table 4. **Use of agricultural areas by active polecats**

Individual	Total records active	% of records in agricultural area	% of home range agricultural area	χ^2
Dickkopf	468	1.07	42	187.1
Phlegma	30	0.00	a	—
Methusalem	74	6.76	67	40.5
Urs	154	0.00	45	69.0
Schaggeli	77	0.00	20	12.0
Mülla	147	3.40	66	85.3
Micro	163	0.00	0	—
Jean-Marc	130	6.15	27	20.8
Paul	243	5.35	44b	82.6
Claude	22	0.00	44c	10.0
Philippe	14	0.00	44c	6.0

a: All records in a barn and a rubbish dump in a distance of about ca. 2 km; in-between agricultural land; b: Polygon calculated excluding an excursion of about 8 km; c: Offer assumed to be the same as for "Paul" within whose polygon they were recorded.
It is assumed that all areas within the minimum-convex-polygon of its records are potentially accessable to an individual polecat. Significance of avoiding agricultural areas was calculated by χ^2-tests ($\chi^2_{(1;p\,0.02)} = 5.4$; $\chi^2_{(1;p\,0.01)} = 10.8$)

Thus, prey remains from different habitat types would not be expected to be found in a single scat.

For 51 daytime resting places there are monitoring data from the previous night, with more than 80 % use of only one habitat type. Table 5 shows that resting sites were mostly found in the same habitat where the activity of the previous night had taken place. Scats which were found in forests or dumps therefore contain with a high probability remains of prey which had been hunted in the same habitat. Scats from buildings may also contain prey remains from other habitats.

It follows that habitat-specific food spectra can be calculated, based on the habitats in which scats of radiotracked polecats were found (Fig. 3). As eggs do not often leave recognizable remains in scats (Brugge 1977; Weber 1988a), their proportion in the

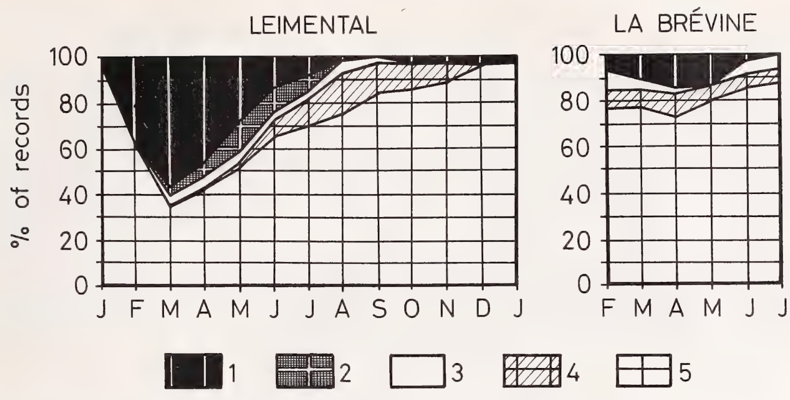


Fig. 2. Use of different biotopes by active polecats through the year. Given are gliding means over three months, excluding rubbish dump records. 1 = farms; 2 = other human settlements; 3 = agricultural land; 4 = hedges, ditches, fallow land; 5 = forest. Numbers of records for single months (Leimental/La Brévine mountains): J 121/0; F 43/68; M 114/90; A 76/118; M 24/3; J 117/37; J 65/93; A 84/0; S 0/0; O 48/0; N 75/0; D 40/0

Table 5. **Habitats where polecats had their daytime resting places and habitats of activity in the previous nights**

Resting site	Activity bout Forest, fallow	Farm, house	Rubbish dump
Forest, fallow	30 (27)	0	0
Farm, house	6 (4)	8 (6)	1 (1)
Rubbish dump	0	0	6 (4)

The table contains the number of activity bouts with more than 80 % of records within the same habitat category. Numbers of activity bouts with all records in the same habitat are given in brackets

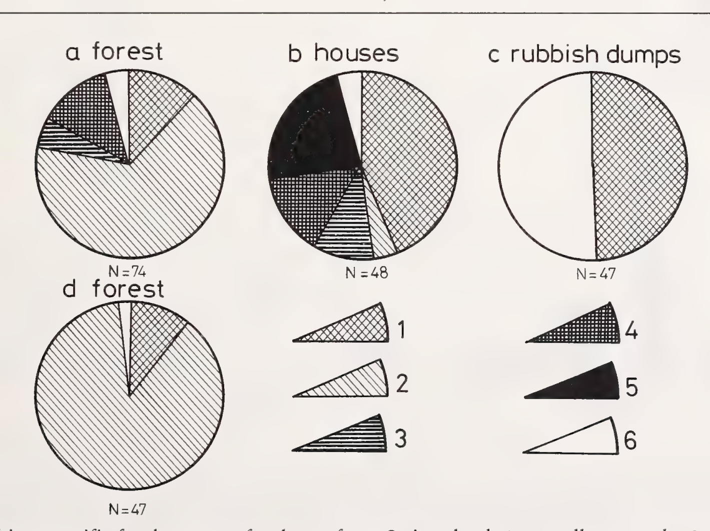


Fig. 3. Habitat-specific food spectra of polecats from Switzerland. 1 = small mammals; 2 = anurans; 3 = other vertebrates; 4 = invertebrates, fruits; 5 = eggs; 6 = carrion, offal. The circle segments are in proportion to the concerned food category in the total diet. Lowland study area: a, b, c; and mountain area: d

"buildings" spectrum is underestimated. On the other hand, this spectrum also contains prey from forests and dumps.

In the Leimental area, the anurans were mainly common frogs *(R. temporaria)*, in the La Brévine mountains mainly common toads *(B. bufo)*. Frogs and toads dominate the "forest" spectrum throughout the year. Their proportion is in winter (Dezember to February) only slightly less important than during the rest of the year (60 % compared to 69 %; χ^2 = 0.47; $p > 0.1$). Mammals are mostly hunted in and around buildings, with woodmice (*Apodemus* sp.) being the most frequent species. 14 of 19 *Apodemus* and 4 of 6 *Microtus* were found in scats from buildings. Mammals from dumps are mostly rats (14 *Rattus norvegicus*; 5 *Apodemus* sp.; 2 *Microtus* sp.; 2 *Glis glis*).

I also found the following uneaten remains of polecat meals: 6 chicken- and 3 turkey-eggs in barns; 4 passerine birds, 25 common frogs and 5 or 6 common toads in forests.

Foraging movements

All radio-tracked polecats were mostly nocturnal (Weber 1987). Daytime activity occurred in summer and autumn. Activity bouts alternated with resting periods also during night-time. To describe foraging, only data from activity bouts of at least 30 min will be used in this section.

The polecats rarely moved by bounding in the typical mustelid manner. Most of their activity was spent "rummaging" ("stöbern", Herter 1959). Hereby they walk in a hasty, irregular and undirected way, holding their head near the ground. They often change direction and investigate even the smallest holes with the muzzle, or move it under the vegetation and leaf litter. This kind of movement is accompanied by much rustling, snuffling, snorting and sneezing which allows rummaging polecats to be easily detected. I never saw polecats leave the ground to climb trees or other structures.

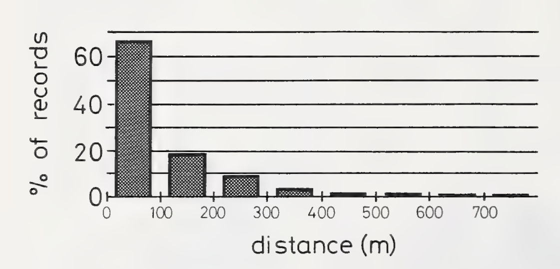


Fig. 4. Minimal distances between consecutive (10 min.) locations of active polecats (N = 1192)

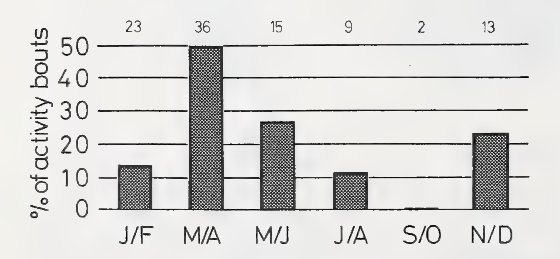


Fig. 5. Proportions of activity bouts during which at least once a distance of ≥ 300 m was run by male polecats. The total numbers of activity bouts observed for each two month period is given at the top of the columns. The difference between the period March to June to the rest of the year is significant (χ^2 = 9.73; $p < 0.01$)

Long distance, strongly directed locomotion was seldom observed (Fig. 4). Only in 3 of 36 observed activity bouts of females distances of at least 300 m were crossed within 10 min. Male polecats showed such behaviour especially during the mating season in spring (Fig. 5). During this period they do not eat much, but live mainly of fat reserves (Weber 1988b). Longdistance, fast and directed movements were also associated with habitat

Table 6. **Characteristics of polecat foraging bouts in different habitat types**

Habitat	Activity bouts (N)	Duration (min)	Total distance (m)	Mean speed (m/min)	Range (ha)
Forest	58 (25)	86 ± 51	508 ± 436	6.16 ± 3.51	3.118
Farms, houses	19 (4)	59 ± 31	76 ± 125	1.22 ± 2.25	0.120
Rubbish dump	16 (6)	86 ± 61	128 ± 293	0.94 ± 1.78	0.068
Mixed	7 (2)	90 ± 50	494 ± 431	5.82 ± 4.76	3.732

Arithmetic means and standard deviations are given. Activity bouts were attributed to the habitat in which at least 80 % of the records were registered. The beginning or the end of an activity bout was often missed. The number of such bouts is given in brackets. Durations, distances, speeds and ranges were calculated including such bouts. Therefore, these data represent minimum values rather than exact means. Ranges were calculated using the standard-circle method (Trevor-Deutsch and Hackett 1980)

changes (6 of 12 activity bouts with habitat changes showed distances of ≥ 300 m within 10 min, compared to 26 of 121 bouts within the same habitat type; $\chi^2 = 4.86$; $p < 0.05$).

Activity bouts without movements of ≥ 300 m within 10 min are interpreted as foraging bouts. Some characteristics of foraging bouts are given in Table 6. As distances were calculated on the basis of a 50 m-grid protocol, total distance and speed values are minima. These data are presented to illustrate the fact, that during a single foraging bout, small areas are intensively exploited, whereby the polecats do not go far from their starting point. This is most extreme while foraging in and around houses.

When foraging in forests, the areas in which a polecat rummaged changed with foraging bouts more or less continuously. This resulted in long-term home ranges much larger than the ranges of single activity bouts (Fig. 6). Extended stays in human settlements were

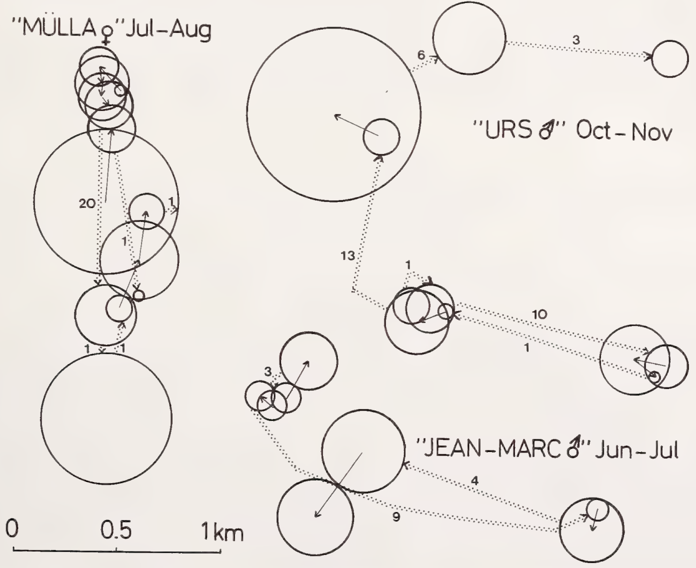


Fig. 6. Ranges of three different polecats during activity bouts in forests (standard circles, Trevor-Deutsch and Hackett 1980). Each circle represents one activity bout. Consecutive bouts during each period of observation are connected by solid arrows. Non-observed movements between area of activity are represented by dotted arrows. Numbers beside dotted arrows give periods between observations in days

nearly always restricted to the interior and the nearest surroundings of single houses or farms. Hereby, the polecats concentrated their activities on a limited number of places: During 18 foraging bouts the male "Dickkopf" used only three different barns. He did not leave one barn during all 5 bouts observed in February and early March, and he was not found resting anywhere else during this period. The use of rubbish-dumps was similar to that of buildings. During 14 of 17 monitored activity bouts the female "Micro" used one single dump exclusively and the male "Urs" did not leave another dump during one week for all 4 observed bouts.

Table 7. **Ranges of individual polecats during single foraging bouts and over longer periods**

Individual	Observation period	N foraging bouts	Single bout range (ha)	Total range (ha)	"Good habitat" (ha) within total range
Dickkopf	22. 12.– 9. 6.	33	2.3	1178.6	312.8
Methusalem	27. 3.–11. 4.	5	0.4	238.2	63.3
Urs	21. 10.–29. 11.	9	1.8	368.6	197.8
Schaggeli	24. 4.–14. 7.	6	0.6	8.3	5.2
Mülla	24. 7.–23. 8.	10	3.1	237.8	69.4
Micro	5. 9.–25. 10.	18	0.3	8.3	8.3
Jean-Marc	13. 6.– 9. 7.	12	3.4	69.0	50.6
Paul	12. 2.–16. 4.	6	1.3	346.3	193.8

Mean single bout ranges calculated as standard circles, total ranges as minimum-convex-polygons (Trevor-Deutsch and Hackett 1980). "Good habitat" is the total surface of forest, fallow, and rubbish dumps within individual total ranges (see Table 3)

The small areas used during single foraging bouts are in contrast to the large home ranges calculated for longer periods (Table 7). This is also valid when only forests and the parts of villages actually exploited within the polygons are considered. The restricted range of the female "Schaggeli" may be due to her cub-rearing during the observation period. She was bound to her den and could not nomadize like the other individuals. During the 7 weeks of observation, the activities of female "Micro" were almost restricted to one single dump.

Discussion

Prey-specific foraging

The predatory behaviour of captive polecats, ferrets and hybrids thereof has been studied by different authors (Goethe 1940; Räber 1944; Herter 1953; Eibl-Eibesfeldt 1956; Wüstehube 1960; Gossow 1970; Apfelbach 1973; Apfelbach and Ebel 1975; Apfelbach and Wester 1977). According to Gossow (1970), the behavioural sequence can be divided into 7 units: 1. Searching; 2. Acoustical, visual or olfactorical perception of prey stimulus; 3. Localisation of stimulus, approaching; 4. Aimed leap at the prey or short pursuit and grasp, repeated if necessary; 5. Killing-bite and follow-up bites; 6. Holding the prey as long as this is still able to wriggle; 7. Carrying away, eating or hiding the prey. As in other mustelids (e.g. Powell 1979 for *Martes pennanti*), foraging economics in polecats may depend chiefly on the success in finding and grasping prey, whereas the killing and eating can be regarded of neglectable importance. Different prey types impose different foraging problems.

My polecats reacted with excitement and appetence behaviour to the scent of rodents. This was already observed by Apfelbach (1973). When mouse or vole scent-tracks were crossed, they were followed, and the prey was found with high probability (see also Herter 1959). Attacks are mainly provoked by visual or acoustical short-distance stimuli

(Apfelbach and Wester 1977; Herter 1959). Rodents avoid being attacked by immobility (Goethe 1940) or by escaping into holes or up trees and shrubs. In my experimental environment similarly structured to the sites where polecats forage outside houses, mice and voles showed a high success rate in avoiding polecat attacks. It must be stressed that this occurred in an experimental environment which facilitated polecat hunting success, as there were no secure escape routes for the prey, and the rodents were unfamiliar with the environment. Under natural conditions, rodent-hunting by polecats may be even less successful, as polecats move around noisily, which allows the prey to escape to secure places even before an attack occurs.

One can conclude that for polecats, finding rodents is a smaller problem than catching them. The hunting experiments show, that rodent-catching is easier on unstructured, bare ground. The radio-tracked polecats hunted rodents mainly inside barns and other buildings, sometimes foraging in the same farm for several weeks.

Although I made no such observations, I believe that rats are followed into their tunnels and caught there, as this has been observed for rabbits (Goethe 1940).

Catching frogs or toads raises completely different problems. Once found and attacked by a polecat, anurans never attempted to escape and were grasped as if they were dead. This is confirmed by observations of Herter (1953). He also emphasizes that polecats do not find frogs by following scent tracks, but more or less by chance, while rummaging around. This is confirmed by my observations and those of Gossow (1970). Sometimes, especially in winter, frogs were dug from their holes in the ground. It remains unclear how the polecats found these sites, especially during winter, with snow-depths of more than one metre. However, anurans are the most important component of polecat winter diet in mountainus areas of Switzerland (Weber 1988a).

One can conclude that anuran hunting for polecats is principally a problem of finding, not of catching. Anurans are not hunted, but collected. Anuran collecting occurred mostly in forests. Hereby, the polecats foraged in small areas, which were intensively searched for frogs and toads during one or more activity bouts, and then abandoned. Consequent foraging bouts concentrated on other areas. The next visit to an abandoned anuran foraging ground may only occur after several weeks or months. This suggests that anuran-collecting polecats are exhaustive predators, that empty a site and then forage elsewhere. This assumption is supported by the radio-tracking results of Nilsson (1978) and Herrenschmidt (1982).

Other important food for Swiss polecats, apart from rodents and anurans, are carrion, offal and eggs. These pose problems of locating and not catching, which is also the case for the seldom eaten birds (found dead) and invertebrates.

Surplus killing

Polecats are known to store prey, mostly anurans, in caches (Danilov and Rusakov 1969; for other authors see Grossenbacher and Neuenschwander 1978). In those frog-heaps found during this study, some of the prey animals were still alive. Similar observations led to the conclusion that polecats bite frogs in a special way producing paralysis, which can be considered as a sophisticated technique of prey-caching (Wüstehube 1960). Gossows's (1970) findings suggest however that paralysis is rather an accidental occurrence.

However, even when the frogs are killed, the question of the function of frog-caching remains. One crucial point is the fact that frog-caches are often not revisited and used as food (e.g. Grossenbacher and Neuenschwander 1978). Herter (1959) therefore interpretes anuran caching as a non-adaptive consequence of an unusual stimulus situation in cases of local concentrations of frogs: Polecats would not stop killing as long as the according releasing mechanism is elicited by the sign stimulus "prey". But Oksanen (1983) and Oksanen et al. (1985) show convincingly that surplus killing can be adaptive, even

when surplus prey is only rarely eaten at all, when this does not significantly reduce future prey availability, and when hunting efforts are not too high.

These conditions are probably fulfilled in the case of polecats and anurans. When a frog is already found, the only effort to kill (or immobilize) is a bite. As the finding of frogs is difficult, the chance of encountering the same frog later is not high. The polecat will presumably not return to the same place until some weeks or months later, and frog mortality is high (about 50 % per year in adult *R. temporaria* according to Heusser 1970). *R. temporaria* needs at least 3 years to maturity in lowlands (Ashby 1969) and up to 9 years in Swiss mountains (Grossenbacher pers. comm.), and even longer to reach maximum size. Additionally, the number of metamorphosed frogs may depend more on the ecological parameters of the spawning pond than on the number of spawning adults (Hintermann 1984). Therefore, killing surplus frogs probably does not strongly influence frog availability in future years. The killing and hoarding of already located anurans may therefore cost a polecat only the time spent, and could be adaptive, even if the prey is rarely eaten. Frog-caches could functionally be considered as a short-term insurance against food shortages. Additionally, surplus killing allows a polecat to eat only the best-tasting parts of anurans, which are, according to my observations, the legs.

The need to decide

Korhonen et al. (1983) found no difference in the basal metabolic rates of polecats and mink *(Mustela vison)*. According to Farrell and Wood (1968), a mink of 1 kg needs about 250 kcal of metabolizable energy per day. Assuming that 75 % of the energy intake is metabolizable (as found by Moors (1977) for mice fed to weasels, *Mustela nivalis*), a mean polecat of 1 kg would need approximately 8 to 10 wood mice or voles, the same number of adult common frogs or toads, 4 chicken eggs or 350 g of commercial cat food per day (Energy contents of prey estimated from data from Robbins 1983 and Moors 1977). This corresponds roughly to the food consumption of my captive polecats, and is more than the quantities proposed by Usinger (1960).

A hungry polecat must decide where to go, what to search and which foraging behaviour to perform. Unspecialized, erratic foraging will probably not result in a sufficient food intake, as different foods must be found and caught in different ways, as different food types occur in different habitats, and as foraging efficiency on the same prey might differ according to the habitat where a polecat hunts. That polecats do not forage randomly is suggested by the demonstration of a searching image in ferrets *(Mustela putorius furo)* by Apfelbach and Ebel (1975).

As discussed in the section above, a polecat following mouse tracks will have only minimal chances of finding a sufficient number of frogs. On the other hand, a frog-hunting polecat ploughing with its nose under leaf-litter and rummaging around will chase away potential small rodent prey. As indicated by the food spectra from forests, polecats concentrate on anuran prey there throughout the year. Even in early winter, when rodent numbers are still high and anurans hibernate underground, rodent predation rarely occurs in forests.

Foraging in barns and around houses minimizes the chances of finding frogs. Here, a polecat has to decide whether to search for eggs or pet food, or whether to hunt rodents. Which option he takes will depend on the relative availability of these potential foods. The food spectra show that all these resources are exploited, and I speculate that polecats only rarely hunt rodents if there are eggs and meat available. However, I do not have the data to support this idea.

In rubbish dumps the polecats must decide whether to kill rats or to search for offal. Again, there are no data to illustrate the relative attractivity of these options.

It follows that Swiss polecats must chose between 5 foraging options, which mutually

exclude one another. There are two hunting options, namely 1. small rodents inside or around houses and 2. rats in rubbish-dumps; and three collecting options, 3. anurans in forests, 4. eggs or meat in or around houses and 5. offal in dumps. In other areas a further option exists: hunting rabbits in their burrows (Goethe 1940; Brugge 1977). The observed foraging behaviour reflects the decisions among these possibilities, and for an understanding of the decisions it is sensible to assume that they are the result of an optimation of related fitness costs and benefits (Krebs and Davies 1981).

Swiss polecats as specialized anuran foragers

The food spectra of the radio-tracked polecats are very similar to those resulting from gut analysis of 120 polecat carcasses from all over Switzerland (Weber 1988a). This is as valid for the relative importance of different food components as for seasonal and altitudinal differences in diet. Therefore, some generalisations on foraging can be formulated on the basis of the results presented here.

Rubbish-dumps were used without obvious seasonal preferences. A female almost never left a small dump during two months of observation. Around this dump was a forest where another female lived on anurans. Rubbish dumps were the best places for catching polecats (author's unpublished data), as many different individuals from the surrounding area visited them regularly. I conclude that, throughout the year, foraging on rubbish dumps may be the most attractive option for Swiss polecats. However, such dumps are rare in our country and only small number of polecats has a dump available. I have no information on the relative attraction of rats and offal at these places.

According to Niethammer and Krapp (1982) and Geuse et al. (1985), the total biomass of ground-living rodents in a European lowland deciduous forest can be estimated as approximately 6000 g/ha in late autumn. Locally, this figure may be several times higher. The biomass of adult common frogs *(R. temporaria)* in Swiss lowland forests would be about 250 g/ha, reaching 750 g/ha in the best places (Grossenbacher 1974, 1980). Thus, the specialisation on anurans by polecats foraging in forests cannot be explained by the quantity of prey available. It must be a result of difficulties in rodent-hunting, as is suggested by the results of my hunting experiments. Finding hibernating anurans in winter may be facilitated by local concentrations of these animals near spawning sites.

The seasonal habitat change in polecats was already known by Tschudi (1858). Further references are given by Gautschi (1983). This habitat change is also a dietary change: In late winter and spring my polecats ceased to forage for amphibians in forests, at least partly, and lived on eggs, offal and small mammals, which they found in and around houses. This is confirmed by seasonal food spectra from Switzerland which resulted from gut analysis (Weber 1988a). At a first glance, this may well be explained by a low availability of frogs and toads during winter, and by concentrations of small mammals in barns during this period. However, for two reasons, I do not consider food availability to be the ultimate cause of the seasonal habitat change in polecats:

1. The habitat change is not synchronous with relative anuran and rodent availability: Anurans hibernate from December to mid-March, their availability probably being highest at spawning sites during March. Rodents may enter human buildings in December, and their numbers will decline until spring, as no reproduction occurs, and as predators, e.g. cats and Beech martens, will kill a certain proportion. If food availability were the cause of habitat change one would expect polecats to enter barns in December and leave them in March. The data of this study show that they entered the buildings during January and partly remained there until early summer.
2. In the mountainous regions, where frog-hunting during winter is especially difficult due to deep snow, the polecats continued to forage for anurans, but used barns for

resting and sleeping. There, the seasonal habitat change takes also place, but the dietary change only to a lesser extent. Consequently, each night, the polecats were obliged to travel longer distances between hunting grounds and resting sites than in summer, when a polecat may sleep near its prey in forests (Weber in press).

My conclusion is that Swiss polecats are specialized anuran foragers, and that other prey is found accidentially while hunting frogs or toads. Only two reasons for specialised foraging on other prey occur: First, extreme local concentrations of potential food (e.g. rubbish dumps, carcasses, hen houses with eggs, peaking microtine populations) can prevent a polecat from frog-hunting throughou the year. Second, a food availability at the barn used for resting in winter (because of thermoregulatory problems, Weber in press) that outweighs the travelling costs between the barn and potential anuran hunting grounds. This situation is more often found in the lowlands, where farms are occupied all year, and therefore offer eggs, pet food and offal in winter, than in the mountains, where stables and barns are sometimes only used during summer. Additionally, in the lowlands higher rodent densities in barns can be expected than in the mountains, as arable farming results in higher food availability for rodents than hay-cutting.

Acknowledgements

I thank U. Rahm for encouraging me to undertake this study, and C. Mermod for valuable advice and encouragement. J.-M. Weber, P. Marchesi, V. Blattner and K. Bieri helped capture polecats. P. Marchesi and M. Borboen provided a sleeping opportunity in the Jura mountains. The hunting societies of Rodersdorf, Leymen, Therwil and Oberwil kindly permitted polecat-trapping in their territories, and the governmental authorities of Neuchâtel, Basel-Landschaft and Solothurn gave all permission to capture and mark animals. J. Taylor corrected the English.

This study is part of a Ph.D. thesis at the University of Basle, which was directed by U. Rahm. The research was supported by the "Basler Stiftung für die biologische Forschung" and the "Brunette-Stiftung für Naturschutz". This paper was written with a grant of the "Geigy-Jubiläums-Stiftung".

Zusammenfassung

Zum Ernährungsverhalten des Iltisses (Mustela putorius L.) in der Schweiz

Das Ernährungsverhalten wurde bei 12 sendermarkierten Iltissen in einem Berggebiet und einem tiefgelegenen Feld-Wald-Siedlungs-Mischgebiet in der Schweiz beobachtet. Zusätzliche Informationen lieferte die Beobachtung einiger Iltisse, die in einem Freiland-Gehege gehalten wurden. Mit diesen Tieren wurden auch einige einfache Experimente durchgeführt.

Es werden fünf verschiedene Möglichkeiten beschrieben, die den Iltissen zur Ernährung offenstehen: 1. Jagd auf Kleinsäuger in und um Gebäude; 2. Jagd auf Ratten auf Müllkippen; 3. Sammeln von Fröschen oder Kröten in geeigneten Wäldern; 4. Sammeln von Eiern, Haustierfutter oder Fleischabfall in und um Gebäude; 5. Sammeln von Fleischabfall auf Müllkippen.

Mindestens drei dieser Optionen können nicht gleichzeitig wahrgenommen werden, weil dazu verschiedene Biotope aufgesucht werden müssen. Außerdem muß ein Iltis entsprechend der jeweiligen Beute sein Jagdverhalten wählen: Kleinsäuger sind leicht zu finden, aber schwer zu fangen, während Froschlurche schwer zu finden, aber leicht zu fangen sind. In den meisten Fällen sind schweizerische Iltisse Froschfresser. Dementsprechend verhalten sie sich nicht wie Jäger, sondern wie Sammler: Ein kleinflächiges Gebiet wird intensiv abgesucht und anschließend verlassen. Es kann mehrere Wochen oder Monate dauern, bis der Iltis wieder zurückkehrt. Das resultierende Raumnutzungsmuster kann am treffendsten mit dem Begriff „nomadisch" charakterisiert werden.

Das beobachtete Auftreten der verschiedenen Ernährungsmöglichkeiten wird diskutiert und mit der folgenden Hypothese erklärt: Schweizerische Iltisse sind Anuren-Spezialisten, weil sie für die Kleinsäugerjagd zu ungeschickt sind. Es gibt zwei Gründe, von dieser Spezialisierung abzuweichen: 1. Extreme lokale Konzentrationen anderer Nahrung (z. B. Müllkippen, Tierkadaver, Hühnerhäuser) können ergiebiger sein als Wälder mit Fröschen. 2. Im Winter, wenn Iltisse aus Gründen der Thermoregulation in Gebäuden ruhen, können die Weg-Kosten zwischen Versteck und Amphibien-Jagdgründen so hoch werden, daß es sich mehr lohnt, in unmittelbarer Umgebung des Versteckes Kleinsäuger zu jagen oder nach Eiern, Fleischabfall oder Haustierfutter zu suchen.

References

APFELBACH, R. (1973): Olfactory sign stimulus for prey selection in polecats (*Putorius putorius* L.). Z. Tierpsychol. **33**, 270–273.

APFELBACH, R.; EBEL, K. (1975): Vom Suchbildverhalten des Frettchens (*Putorius furo*) beim Beutefang. Z. Säugetierkunde **40**, 378–379.

APFELBACH, R.; WESTER, U. (1977): The quantitative effect of visual and tactile stimuli on the prey-catching behaviour of ferrets *(Putorius furo)*. Behav. Process. **2**, 187–200.

ASHBY, K. R. (1983): The population ecology of a self-maintaining colony of the common frog *(Rana temporaria)*. J. Zool. **158**, 453–474.

BREHM, A. (1879): Illustrirtes Thierleben. 4. Aufl. (Hrsg. O. Zur Strassen). Leipzig: Bibliographisches Institut.

BRUGGE, T. (1977): Prooidierkeuze van wezel, hermelijn en bunzing in relatie tot geslacht en lichaamsgroote. Lutra **19**, 39–49.

DANILOV, P. I.; RUSAKOV, O. S. (1969): (Special aspects of the ecology of the polecat *(Mustela putorius)* in the north-west regions of the European U.S.S.R.). Zool. Zh. **48**, 1383–1394.

EIBL-EIBESFELDT, I. (1956): Angeborenes und Erworbenes in der Technik des Beutetötens (Versuche am Iltis). Z. Säugetierkunde **21**, 135–137.

FARRELL, D. J.; WOOD, A. J. (1968): The nutrition of the female mink *(Mustela vison)*. II. The energy requirements for maintenance. Can. J. Zool. **46**, 47–52.

GAUTSCHI, A. (1983): Nachforschungen über den Iltis (*Mustela putorius* L.). Schweiz. Z. Forstwesen **134**, 49–60.

GEUSE, P.; BAUCHAU, V.; LE BOULENGE, E. (1984): Distribution and population dynamics of bank voles and wood mice in a patchy woodland habitat in central Belgium. Acta Zool. Fenn. **173**, 65–68.

GOETHE, F. (1939): Untersuchungen über die Winternahrung des Iltis nebst einigen weiteren biologischen Feststellungen. Wild und Hund **43**, 720–722.

— (1940): Beiträge zur Biologie des Iltis. Z. Säugetierkunde **15**, 180–221.

GOSSOW, H. (1970): Vergleichende Verhaltensstudien an Marderartigen I: Über Lautäußerungen und zum Beuteverhalten. Z. Tierpsychol. **27**, 405–480.

GRASHEY, O. (1894): Praktisches Handbuch für Jäger. Stuttgart: Hoffmann.

GROSSENBACHER, K. (1974): Die Amphibien der Umgebung Berns. Mitt. Naturforsch. Ges. Bern NF **34**, 1–64.

— (1980): Beitrag zur Populationsdynamik des Grasfrosches *Rana temporaria*, nebst Bemerkungen zur Erdkröte *Bufo bufo* (Amphibia, Anura). Jahrb. Nat. Hist. Mus. Bern **7**, 177–193.

GROSSENBACHER, K.; NEUENSCHWANDER, U. (1978): Iltis *(Putorius putorius)* tötet Erdkröten *(Bufo bufo)*. Jahrb. Nat. Hist. Mus. Bern **6**, 171–176.

HAINARD, R. (1948): Les mammifères sauvages d'Europe. Vol. 1. Neuchâtel: Delachaux et Niestlé.

HERRENSCHMIDT, V. (1982): Note sur les déplacements et le rythme d'activité d'un putois, *Mustela putorius* L., suivi par radiotracking. Mammalia **46**, 554–556.

HERTER, K. (1953): Über das Verhalten von Iltissen. Z. Tierpsych. **10**, 56–71.

— (1959): Iltisse und Frettchen. Wittenberg/Lutherstadt: Neue Brehm Bücherei, Ziemsen Vlg.

HINTERMANN, U. (1984): Populationsdynamische Untersuchungen am Grasfrosch *Rana temporaria* LINNAEUS, 1758 (Salientia, Ranidae). Salamandra **20**, 143–166.

HEUSSER, H. (1970): Ansiedlung, Ortstreue und Populationsdynamik des Grasfrosches *(Rana temporaria)* an einem Gartenweiher. Salamandra **6**, 80–87.

KORHONEN, H.; HARRI, J.; ASKAINEN, J. (1983): Thermoregulation of polecat and raccoon dog: A comparative study with stoat, mink and blue fox. Comp. Biochem. Physiol. **74A**, 225–230.

KRATOCHVIL, J. (1952): O potravě a rasách tchoře tmavého (*Putorius putorius* L.). Acta Univ. Agriculturae Silviculturae Brno **1**, 43–60.

KREBS, J. R.; DAVIES, N. B. (1981): An introduction to Behavioural Ecology. Oxford: Blackwell.

LABHARDT, F. (1980): Zur Fütterungstätigkeit und über einige Verhaltensweisen einer freilebenden Iltisfähe, *Mustela putorius* LINNE, 1758. Säugetierkundl. Mitt. **28**, 247–251.

MERMOD, C.; DEBROT, S.; MARCHESI, P.; WEBER, J.-M. (1983): Le putois (*Mustela putorius* L.) en Suisse romande. Rev. Suisse Zool. **90**, 847–856.

MOORS, P. J. (1977): Studies of the metabolism, food consumption and assimilation efficiency of a small carnivore, the weasel (*Mustela nivalis* L.). Oecologia **27**, 185–202.

NILSSON, T. (1978): Home range utilization and movements in polecat, *Mustela putorius*, during autumn. II. Congr. Theriol. Int., Brno, CSSR, June 20–27, 1978, 13.

NIETHAMMER, J.; KRAPP, F. (1982): Handbuch der Säugetiere Europas. Band 2/I. Wiesbaden: Akademische Verlagsgesellschaft.

OKSANEN, T. (1983): Prey catching in the hunting strategy of small Mustelids. Acta Zool. Fennica **174**, 193–196.

OKSANEN, T.; OKSANEN, L.; FRETWELL, S. T. (1985): Surplus killing in the hunting strategy of small predators. Am. Nat. **126**, 328–346.

Powell, R. A. (1979): Ecological energetics and foraging strategies of the fisher. J. Anim. Ecol. **48**, 195–212.
Raeber, H. (1944): Versuche zur Ermittlung des Beuteschemas an einem Hausmarder *(Martes foina)* und einem Iltis *(Putorius putorius)*. Rev. Suisse Zool. **51**, 293–332.
Rahm, U. (1976): Die Säugetiere der Schweiz. Veröff. Nat. Hist. Mus. Basel **9**, 1–87.
Robbins, C. T. (1983): Wildlife feeding and nutrition. New York: Academic Press.
Rohrdorf, H. C. (1835): Der Schweizer-Jäger. Glarus: F. Schmid.
Rzebik-Kowalska, B. (1972): Studies on the diet of the carnivores in Poland. Acta Zool. Cracoviensia **17**, 415–506.
Trevor-Deutsch, B.; Hackett, D. F. (1980): An evaluation of several grid-trapping methods by comparison with radio telemetry in a home range study of the eastern chipmunk. In: A handbook of biotelemetry and radio tracking. Ed. by C. J. Amlaner and D. W. MacDonald. Oxford: pergamon Press. 375–386.
Tschudi, F. (1858): Das Tierleben der Alpenwelt. Leipzig: Weber.
Usinger, A. (1960): Einheimische Säugetiere und Vögel in der Gefangenschaft. Hamburg: Parey.
Walton, K. C. (1977): Polecat. In: The handbook of British mammals. 2nd ed. Ed. by G. B. Corbet and H. Southern. Oxford: Blackwell. 345–352.
Weber, D. (1987): Zur Biologie des Iltisses (*Mustela putorius* L.) und den Ursachen seines Rückganges in der Schweiz. Diss. Universität Basel.
— (1988a). The diet of polecats (*Mustela putorius* L.) in Switzerland. Z. Säugetierkunde **53** (in press).
— (1988b). Einige Daten zu Größe und Kondition schweizerischer Iltisse *Mustela putorius* L. Säugetierkundl. Mitt. **34** (in press).
— (in press): The ecological significance of resting sites and the seasonal habitat change in polecats *(Mustela putorius)*. J. Zool.
Wüstehube, C. (1960): Beiträge zur Kenntnis besonders des Spiel- und Beuteverhaltens einheimischer Musteliden. Z. Tierpsychol. **1**, 579–613.

Author's address: Dr. Darius Weber, Hintermann & Weber, Öko-Logische Beratung & Systemanalysen, Hauptstraße 44, CH-4153 Reinach, Switzerland

Z. Säugetierkunde 54 (1989) 393–396
© 1989 Verlag Paul Parey, Hamburg und Berlin
ISSN 0044-3468

Distribution actuelle du chevreuil *(Capreolus capreolus)*, du daim *(Dama dama)* et du cerf *(Cervus elaphus)* en Espagne

Par F. Braza, I. Varela, C. San José et V. Cases

Estación Biológica de Doñana, Sevilla, España

Reception du Mr. 5. 4. 1988

Abstract

Present distribution of roe deer (Capreolus capreolus), fallow deer (Dama dama) and red deer (Cervus elaphus) in Spain

By help of questionnaires sent to the respective organisations maps on the present distribution of roe deer, fallow deer and red deer in Spain were elaborated. At the beginning of this century most of these species were extinguished because of bad hunting politics. They were reintroduced in the sixties and, together with rural depopulation and decrease of predators, spread widely.

Introduction

Il n'y a que peu de réferences sur la distribution des espèces de la famille Cervidae: chevreuil *(Capreolus capreolus)*, daim *(Dama dama)* et cerf *(Cervus elaphus)* en Espagne; c'est ainsi que depuis la révision générale de Cabrera (1914) seuls des auteurs comme Niethammer (1963) et Whitehead (1983) incluent quelques informations sur la Péninsule Ibérique.

Bien que la distribution du daim en Espagne ait été publiée par Chapman et Chapman (1980), ces espèces n'ont été revisées récemment que par Niethammer et Krapp (1986) qui se sont inspirés de données préliminaires fournies par nous-mêmes.

Matériel et méthodes

Pour actualiser donc, d'une façon détaillée, la distribution de ces trois espèces de cervidés en Espagne, nous avons préparé une enquète en 1982 et sollicité ainsi les renseignements suivants: présence ou absence de l'animal dans les différentes communes, origine des populations existantes, évolution actuelle de celles-ci et autres informations qui pussent nous être d'intérêt.

Le questionnaire fut envoyé aux organisations compétentes (Institut pour la Conservation de la Nature, Mairies, Associations de Chasseurs etc.) et une fois analysés les premiers résultats obtenus, nous avons redemandé aux mairies des endroits où la présence des cervidés avait été constatée, une information plus précise quant aux limites géographiques de distribution.

Pour corriger enfin, pertinemment, les renseignements accumulés nous avons publié une première esquisse de carte de distribution de ces 3 espèces dans une revue de diffusion nationale.

Bien que pour certains endroits les données soient encore incomplètes, nous espérons que nos résultats puissent servir aux futurs travaux concernant ces cervidés.

Aussi bien aux Baléares qu'aux Canaries on n'a détecté ni chevreuil, ni daim, ni cerf.

Résultats

Le chevreuil *(Capreolus capreolus)* se distribue de façon homogène dans la Cordillère Cantabrique et pénètre dans les montagnes les plus septentrionales des Systèmes Ibérique et Central (Fig. 1). De toutes les populations, celles des Asturies seules semblent être en

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5406-0393 $ 02.50/0

régression tandis que les autres sont plutôt stables et même, dans certains endroits, en augmentation.

Vers le sud, on observe une réduction de la taille des populations et un isolement supérieur; c'est le cas par exemple dans les Montes de Toledo, Sierra Morena et Sierra de Cadix. Selon des données récentes (Braza et al. 1987) les chevreuils de Cadix sont en franche régression bien que certains individus aient colonisé de nouveaux coins de la province de Málaga qui leur offrent une protection plus adéquate. Ces populations représentent la frontière sudoccidentale de la distribution du chevreuil et sont donc très intéressantes pour leur total isolement.

Quand on le compare avec le daim ou le cerf, le chevreuil a été très rarement réintroduit en Espagne sauf dans les Pyrénées Orientales et dans certaines localités des Systèmes Central et Ibérique.

La Figure 2 correspond à la carte de distribution du daim (*Dama dama*). Il s'agit là de populations isolées dues à des réintroductions récentes. Il faut cependant souligner le cas exceptionnel des daims du Parc National de Doñana qui, au XV siècle faisaient l'objet de commerce à titre de bétail (Granados 1987).

Quant au cerf (*Cervus elaphus*) il a été lui aussi réintroduit plus ou moins récemment sauf le cerf des populations de Sierra Morena, Montes de Toledo, Doñana et de quelques autres coins précis de la Cordillère Cantabrique (Fig. 3).

Discussion

Dans la plupart des cas ces espèces s'éteignirent au début de ce siècle à cause d'une très mauvaise politique de chasse, et elles furent réintroduites à partir des années soixante.

Dès cette époque on constate une émigration humaine vers les centres industriels et donc un important dépeuplement des régions montagneuses; cela a du favoriser la grande expansion des populations d'ongulés sauvages en Espagne (Tellería et Sáez-Royuela 1984). D'autre part, la disparition progressive du loup (*Canis lupus*) de la majeure partie du territoire espagnol vers les années 40 (Valverde 1971) a contribué également à l'augmentation du nombre de ces grands mammifères. Cette expansion continue à progresser actuellement sauf pour certaines populations isolées de chevreuils de la Sierra de Cadix. Si nous comparons nos résultats avec ceux de Tellería et Sáez-Royuela (1984) dans le centre de l'Espagne, au début des années 80, nous observons une incursion progressive des cervidés dans de nouvelles zones. Ainsi dans la province de Valladolid où l'on avait constaté l'absence de chevreuil en 1983 (date de notre enquète), vient d'être détectée la présence de cet animal au cours de l'année 1987 (Delibes com. per.).

En général la distribution des cervidés en Espagne a été très conditionnée par l'influence humaine (réintroductions ou exterminations) et c'est pour cela qu'il n'est pas d'un grand intérêt d'analyser avec plus de détail ses relations écologiques.

Remerciements

Pour la réalisation de ce travail nous avons profité de l'appui économique de la «Comisión Asesora Interministerial Científica y Técnica». Nous remercions aussi les organismes qui ont collaboré à la distribution de notre enquète (Institut pour la Conservation de la Nature, Mairies, Associations de chasseurs et la revue de nature «Quercus»).

Résumé

Après enquète auprès des organismes compétents, nous avons élaboré des cartes de distribution actuelle du chevreuil, du daim et du cerf en Espagne. La plupart de ces espèces ont disparu au début du siècle à cause d'une mauvaise politique de chasse mais elles furent réintroduites à partir des années 60;



Fig. 1. Distribution du chevreuil *(Capreolus capreolus)* en Espagne



Fig. 2. Distribution du daim *(Dama dama)* en Espagne

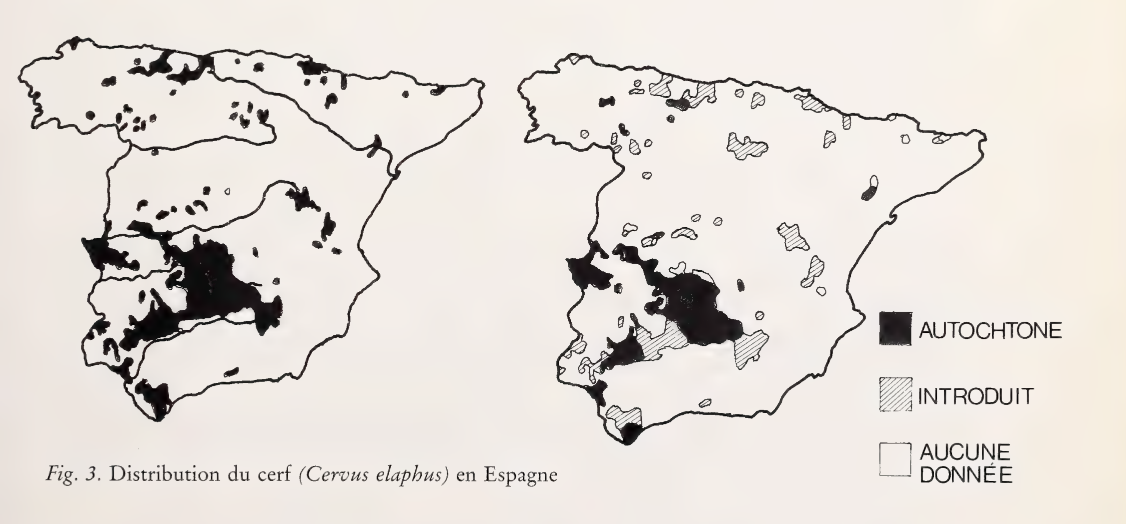


Fig. 3. Distribution du cerf *(Cervus elaphus)* en Espagne

et depuis, elles ont expérimenté une importante expansion qui a coincidé avec le dépeuplement rural et une diminution des prédateurs.

Zusammenfassung

Gegenwärtige Verbreitung von Reh (Capreolus capreolus), Damwild (Dama dama) und Rothirsch (Cervus elaphus) in Spanien

Als Ergebnis einer Umfrage bei den zuständigen Behörden wurden Verbreitungskarten für Reh, Dam- und Rotwild in Spanien gezeichnet. Zu Beginn des 20. Jahrhunderts waren die drei Arten weitgehend ausgerottet. Einbürgerungen in den 60er Jahren, die Landflucht der menschlichen Bevölkerung und die Abnahme der Freßfeinde der Cerviden begünstigten eine erneute Zunahme und Ausbreitung der drei Arten.

Bibliographie

BRAZA, F.; VARELA, I.; ALVAREZ, F. (1987): El corzo en la Sierra de Cádiz. AMA-CSIC. Sevilla.

CABRERA, A. (1914): Fauna Iberica: Mamíferos. Madrid. Museo Nacional de Ciencias Naturales.

CHAPMAN, D.; CHAPMAN, N. (1980): The distribution of fallow deer: A world-wide Review. Mammal Review **10**, 62–138.

GRANADOS, M. (1987): Transformaciones históricas de los ecosistemas del Parque Nacional de Doñana. Tesis. Universidad de Sevilla.

NIETHAMMER, G. (1983): Die Einbürgerung von Säugetieren und Vögeln in Europa. Hamburg, Berlin: Verlag Paul Parey.

NIETHAMMER, G.; KRAPP, F. (1986): Handbuch der Säugetiere Europas. Wiesbaden: Aula-Verlag.

TELLERÍA, J. L.; SÁEZ-ROYUELA, C. (1984): The large mammals of Central Spain. An introductory view. Mammal Review **14**, 51–56.

VALVERDE, J. A. (1971): El lobo español. Montes **159**, 229–241.

WHITEHEAD, G. K. (1982): Deer of the world. Constable. London: 66–101.

Adresse des auteurs: Dr. F. BRAZA, Estación Biológica Doñana, Apdo. 1056, E-41013 Sevilla, España

Z. Säugetierkunde 54 (1989) 397–405

ISSN 0044-3468

Intraspecific Allometry: The Kidney

By H. Hackbarth and K. Gärtner

Zentrales Tierlaboratorium und Institut für Versuchstierkunde, Medizinische Hochschule Hannover

Receipt of Ms. 18. 3. 1988

Abstract

Interspecific and intraspecific allometric relationships between kidney mass and body mass were determined in 4 hamster species, 10 inbred strains of rats and 24 inbred strains of mice. Genetic allometry, as such, was possible on hand from an inherent reduction of genetically based differences by comparing species or strainspecific mean values rather than individual values. Ontogenetic allometry was investigated in growing female individuals of a single inbred rat strain.

The interspecific and intraspecific allometric relationships between kidney and body mass were significant in all cases investigated with the one exception of the intraspecific allometry in the male mouse. This can be explained by an extreme genetic variation between the different inbred strains or species in combination with a narrow range in body weight.

Allometry between the different rat-inbred-strains, however, was statistically significant. The allometric functions within rats (slope males 0.96, females 0.89) and between species (slope 0.85, Prothero 1984) were equivalent. A similar equivalence was, like-wise, found to hold in the ontogenetic allometry (slope 0.82), whereby the intraspecific values for slope and intercept equalled those observed in the interspecific and intraspecific comparisons.

In essence, this study has proven that the investigated mouse-hamster-rat regression displays an allometric function (slope 0.86) statistically equivalent and, therefore, in accordance with the previously established regression for 63 different species of terrestrial mammals (slope 0.85, Prothero 1984). As a result, the general interspecific relationship of kidney mass to body mass which holds true for mammalian species can be transferred onto, and is hence valid in, interspecific and especially intraspecific comparisons of small laboratory rodents.

Introduction

Due to the vital role held by the kidney in water and electrolyte metabolism of the entire organism, there is a close interspecific correlation between kidney mass and total body mass (Calder and Braun 1983). In mammals, Prothero (1984) has numerically expressed the interspecific relationship between kidney mass and body mass in the following allometric equation:

$$\text{kidney mass (g)} = 0.020 \times \text{body mass (g)}^{0.85 \pm 0.01}$$

Similar exponential relationships have been found for glomerular size and number with varying values for the body mass exponent (Rytand 1938). Work by Brody (1945) substantiated these findings.

Among primates (Stahl 1965), an equation nearly identical to Prothero's (1984) comparison of kidney mass to body mass was found. Within adults species of small laboratory animals such as rats (Closkey and Jermanowich 1985) and mice (Hackbarth and Hackbarth 1981), however, either no such relationship could be found, or when present, the body mass exponents differed significantly from those found in interspecies comparisons.

Moreover, within a single inbred strain of mice, the growing kidney did follow the same function for kidney mass as described by interspecific relationship for adults (Hutson et al. 1981).

U.S. Copyright Clearance Center Code Statement: 0044-3468/89/5406-0397 $ 02.50/0

Considering the lack of a consistent allometry between glomerular parameters and body mass, the question arises as to whether the relationship of kidney mass to body mass within a single species of small rodents follows the same function as among different species. Heusner (1982) recently claimed that there is no a priori reason for such a common allometry within a single species, hence any value for the body mass exponent could be expected.

This study was, therefore, conceptualized to determine a possible intraspecific allometry of kidney mass to body mass in small rodent species. Values for the mass coefficient "a" and the mass exponent "b" of the general allometrical function (Huxley 1932):

$$\text{kidney mass} = a \times \text{body mass}^{b}$$

are compared to those found between species.

Furthermore, it should be mentioned, that in accordance with Röhrs (1959), a strong separation was made between ontogenetic and intraspecific allometry. While the ontogenetic allometry, on one hand, was determined by comparing growing individuals of one sex of a single inbred strain of rats, intra- and interspecific allometry was derived from comparisons between mean kidney and body weights taken from each sex of 10 different identically aged inbred strains of rats, 24 identically aged inbred strains of mice and 4 adult species of hamsters. These ontogenetic, intraspecific, and interspecific allometries in small laboratory animals were compared to the interspecific allometry reported by Prothero (1984).

Material and methods

Body mass and kidney mass were determined in five adult females and five adult males of each hamster species and each inbred mice and rat strain. Prior to sacrifice physiological kidney functions were determined (Hackbarth and Hackbarth 1981, 1982; Hackbarth et al. 1981, 1982) and histometrical measurements were performed after sacrifice (Hackbarth et al. 1987). The animals were sacrificed with halothane (hamsters), CO_2-inhalation (rats), or cervical dislocation (mice). Body mass was immediately recorded, and the kidneys were removed, bled by drainage, and weighed.

Prior to sacrifice, all animals were maintained under identical environmental conditions at a room temperature of 22 ± 2 °C, a relative humidity of 55 ± 5 %, and a 12L:12D photoperiod. The rats were kept under controlled micro-biological conditions (specific pathogen free, barrier maintained). All animals were fed a standard laboratory diet.

Interspecific allometry

The kidney and body weights of four hamster species were determined: *Cricetus cricetus, Mesocricetus auratus, Cricetulus griseus* and *Phodopus sungorus* (Table 1). On the day of investigation, *Cricetus cricetus* individuals were 204 days, those of the remaining three species 92–100 days old. At these ages, the animals were considered to be adult.

Intraspecific allometry

Genetic allometry

Body and kidney mass of ten different inbred strains of rats *(Rattus norvegicus)* were recorded (Table 1): ACl/Ztm, AS/Ztm, BH/Ztm, BS/Ztm, DA/Ztm, LEW/Ztm, MWF/Ztm, SC/Ztm, SPRD/Ztm, WC/Ztm. All animals were 110–120 days old. The body weights of the females ranged from 137 to 259 g and those of the males from 185 to 401 g.

Body and kidney mass were recorded for 24 inbred strains of mice at the age of 100 days. For strain designation and mean strain values see Table 1, for further details see Hackbarth and Hackbarth (1981).

Ontogenetic allometry

Body and kidney weights were determined in nineteen females of the inbred strain MWF/Ztm ranging in age from 30 to 50 days of age and in body mass from 67 to 180 g. In a pilot study, this growth period alone proved to follow an allometric relation between kidney and body mass predominantly due to an increase in body mass. Prior to 30 days of age, postnatal development seems to have a greater influence on kidney mass than does body mass (Kittelson 1917). After 50 days, the increase of body mass is more and more a function of increasing body fat.

Statistics

Intraspecies allometry was calculated separately for each species, strain and sex. Following logarithmic transformation of the body and kidney weights, linear regression analysis (Sachs 1984) was performed on the mean values for each species, strain, and sex. By statistically excluding environmental influences (e.g. considering mean values rather than individual weights within one strain), the resulting intraspecific allometries reflect the genetically influenced relationship of kidney to body mass within a species (genetic allometry).

Slope and intercept of the regression were calculated. The mass exponent ("b" ± SD), mass coefficient ("a" ± SD), and coefficient of correlation "r" were calculated for each relationship. The mass exponents and mass coefficients were first tested for significance and subsequently compared with covariance analysis (Sachs 1984). These values were then compared to those of Prothero's (1984) using a simple t-test (Sachs 1984).

Ontogenetic allometry was determined by taking the body and kidney weights of nineteen females of the inbred rat strain MWF/Ztm. Following logarithmic transformation of the individual data, ontogenetic allometry was calculated as described above. This ontogenetic allometry reflects the non-genetically determined variability within the genetically-identical individuals of an inbred strain.

Results

Intraspecific allometry

Ontogenetic allometry (rat)

Growing females of the MWF/Ztm inbred strain clearly exhibit an allometric relationship between kidney mass and body mass. The weight range covered by these animals between 30 and 50 days of age was 67–180 g. Slope and intercept are equivalent ($p > 0.05$) to those found for adult rats as well as for the interspecific relationship (Prothero 1984) (Fig. 1 and Table 2).

Genetic allometry (rat, mouse)

Rat – There is no difference between sexes in the slope or the intercept of the regression lines ($p > 0.05$). There is a large genetic variation within each sex (Fig. 1 and Table 2). The slopes and intercepts do not differ ($p > 0.05$) from those of other intraspecific regressions determined in this study nor from those found in the general interspecific comparison of Prothero (1984).

Mouse – There is a pronounced sex difference in mice. Males clearly lie above the general regression line (see Fig. 1). Within male mice, strain differences among males were large and the body weight range small. Hence, no significant correlation of kidney to body mass was found (Table 2). Only in females a significant allometry was evident (slope 0.54; Table 1). This is statistically different ($p < 0.05$) from other intraspecific and interspecific allometries described in this study as well as from the general interspecific relationship of Prothero (1984).

Within *Mus musculus,* the most obvious difference is the sex difference in kidney mass accompanied by large strain deviations. In general, the weight range is *Mus musculus* in too narrow to allow a reliable statistical analysis. Combining male and female data does not result in a more statistically significant allometry (Hackbarth et al. 1982).

Table 1. **Body weight (g) and kidney weight (g) of strains and species**

mice	**males** $\bar{x} \pm$ **SD**		**females** $\bar{x} \pm$ **SD**	
strain	body weight	kidney weight	body weight	kidney weight
CE/J	36.90± 3.93	0.383±0.028	22.82± 1.27	0.246±0.011
C3D2F_1/J	35.78± 3.44	0.451±0.030	25.79± 1.49	0.262±0.016
AKR/J	34.03± 1.74	0.442±0.042	31.28± 2.18	0.292±0.039
NZB/BINJ	34.00± 1.31	0.415±0.020	27.17± 1.31	0.281±0.009
CBA/J	33.90± 3.68	0.416±0.041	26.30± 3.52	0.244±0.023
ST/bJ	33.62± 3.16	0.374±0.013	25.59± 2.55	0.250±0.015
C3H/HeJ	32.83± 1.18	0.410±0.028	28.95± 3.09	0.265±0.015
B6D2F_1/J	32.72± 3.07	0.377±0.026	21.01± 0.20	0.197±0.006
BuB/BnJ	32.40± 2.33	0.378±0.042	27.48± 1.60	0.292±0.024
CB6F_1/J	31.73± 1.99	0.390±0.032	24.21± 0.88	0.242±0.011
PL/J	31.16± 2.18	0.354±0.036	11.46± 2.12	0.243±0.027
AKD2F_1/J	31.06± 1.79	0.408±0.032	26.92± 2.31	0.258±0.024
B6AF_1/J	30.97± 2.18	0.319±0.019	22.11± 1.89	0.246±0.024
C57Br/cdJ	29.47± 1.91	0.398±0.024	25.22± 0.67	0.284±0.017
Balb/cJ	28.88± 1.84	0.430±0.036	21.58± 1.18	0.231±0.003
CAF_1/J	28.83± 1.84	0.366±0.019	21.83± 1.23	0.226±0.012
SJL/J	27.73± 1.60	0.393±0.038	20.25± 1.43	0.268±0.022
C57BL/6J	27.54± 2.29	0.276±0.033	22.03± 2.13	0.266±0.023
A/J	27.28± 1.54	0.373±0.021	21.97± 1.80	0.237±0.018
DBA/2J	27.06± 2.91	0.401±0.040	26.61± 2.73	0.266±0.019
RIIIS/J	26.91± 1.35	0.319±0.021	18.64± 1.03	0.230±0.006
SWR/J	25.47± 1.11	0.318±0.025	20.71± 1.47	0.247±0.012
RF/J	25.29± 2.26	0.418±0.042	24.62± 1.15	0.314±0.026
SM/J	22.41± 1.92	0.425±0.064	16.96± 1.30	0.198±0.020
rats	**males** $\bar{x} \pm$ **SD**		**females** $\bar{x} \pm$ **SD**	
strain	body weight	kidney weight	body weight	kidney weight
ACI/Ztm	213.37± 8.24	1.910±0.178	160.89± 8.30	1.446±0.156
AS/Ztm	290.97± 8.22	2.900±0.142	175.45± 5.53	1.524±0.139
BH/Ztm	318.24± 18.14	2.882±0.274	230.82± 6.00	2.096±0.085
BS/Ztm	314.47± 23.73	2.052±0.091	179.28± 7.22	1.188±0.056
DA/Ztm	184.97± 8.14	1.508±0.083	137.10±21.28	1.226±0.147
LEW/Ztm	335.20± 24.61	2.826±0.188	190.56± 7.33	1.540±0.068
MWF/Ztm	347.60± 20.69	2.684±0.211	188.67±14.47	1.438±0.105
SC/Ztm	401.45± 31.37	3.508±0.265	259.38± 7.83	2.120±0.086
SPRD/Ztm	382.10± 21.50	3.218±0.306	225.30±13.82	1.738±0.104
WC/Ztm	327.69± 33.36	2.558±0.350	211.02± 5.93	1.569±0.060
hamster	**males** $\bar{x} \pm$ **SD**		**females** $\bar{x} \pm$ **SD**	
species	body weight	kidney weight	body weight	kidney weight
Cricetus cricetus	470.21±135.27	1.922±0.570	333.98±89.83	1.410±0.217
Mesocricetus auratus	116.47± 8.36	0.852±0.013	127.80± 8.89	1.036±0.106
Phodopus sungorus	32.91± 4.48	0.336±0.044	33.86± 3.83	0.330±0.012
Cricetulus griseus	35.79± 4.97	0.320±0.047	25.35± 3.25	0.208±0.179

Interspecific allometry

Hamster – The wide range of body mass covered by these species, facilitates to detect significant correlations, when kidney mass is plotted versus body mass in a double logarithmic system (Fig. 1 and Table 2). There is no significant difference ($p > 0.05$) between the regression lines for males and females. This is evident in figure 1, but not striking. The slope and the intercept of the hamster regression are not significantly different from those for intraspecific regressions of small laboratory animals investigated here or from those found in the general interspecific comparison for mammals of PROTHERO (1984).

Intraspecific versus interspecific allometry

Table 2 summarizes the parameters of the allometric equations, resulting from interspecific and intraspecific comparisons. These values are, furthermore, compared with those published by PROTHERO (1984) for 63 species of mammals. No significant ($p > 0.05$)

Table 2. **Intra- and interspecific allometric parameters**

species	sex	No. of points	b ± SD	ln a ± SD	r	p <
rat	males	10	0.956±0.155	-4.542±0.889	0.909	0.01
	females	10	0.887±0.188	-4.222±0.989	0.858	0.01
rat growing	females	19	0.823±0.035	-3.588±0.172	0.984	0.01
mice	males	24	0.251±0.198	-1.817±0.674	0.261	n.s.
	females	24	0.540±0.119	-3.086±0.376	0.696	0.01
hamster	males	4	0.682±0.044	-3.500±0.203	0.996	0.01
	females	4	0.741±0.117	-3.802±0.524	0.976	0.05
all		95	0.862±0.202	-3.992±0.086	0.976	0.01
Prothero (1984)		117	0.85 ±0.01	-3.912±0.023	0.993	0.01

difference appears between the slopes or the intercepts of the overall intraspecific equation versus that of PROTHERO (1984). With respect to the amount of data contributing to the present analysis, it is surprising that such a limited amount suffices to establish and confirm the close approximation of the regression found in laboratory rodents to that found in the more extensive interspecific comparison.

Discussion

Intraspecific allometry often faces the problem of a limited weight range within a single species. This problem can be solved by reducing variation across the regression to be calculated. The most efficient way to achieve this reduction in variance is by defining intraspecific allometry as was done by RÖHRS (1959). He subdivided intraspecific allometry into:

1. ontogenetic allometry
   a. allometry of an identical growing individual
   b. allometry of growing individuals in one population at various stages of growth
2. intraspecific allometry
   a. allometry of different sized adult individuals of the same population of a single species
   b. allometry of different sized adult individuals of different subspecies.

In the present study, intraspecific allometry of kidney mass to body mass was obtained by comparing different genotypes (inbred strains) of two species (*Mus musculus* and *Rattus norvegicus*). An allometric relationship resulting from this approach is exclusively due to genetic differences between the different inbred strains compared. This genetic allometry within mice and rats contrasts with that of different sized adult individuals of different species; i.e. interspecific allometry (Röhrs 1959).

Ontogenetic allometry (i.e. correlations among growing individuals) was also investigated by comparing individuals of a single rat inbred strain. All animals were of the same genotype, hence the resulting allometry is comparable to that which results from a single growing individual. Despite the small body weight range within each species, the applied experimental design led to significant correlations for the best fit (ln "kidney mass" to ln "body mass") in all species investigated.

Only within male mice genetic variation among inbred strains was so extreme and the weight range so narrow that a significant correlation could not be detected. The high degree of variation within males ruled out any statistical significance. Within females, the body mass coefficient as well as the body mass exponent of the allometric function had large standard deviations (Table 1). An obvious sex difference is, thus, evident in mice. Males have larger kidneys than females at the same relation to body mass. This sex difference in kidney mass has been previously shown to be testosterone dependent (Crabtree 1941). The mass exponent within female mice ($b = 0.54$) is much lower than that of the interspecific allometry (Table 2). Due to the large genetic variation and narrow weight range, however, the difference is only slightly significant ($p < 0.05$), and its value must be carefully interpreted. Nevertheless, most values for inbred strains of mice lie close to the overall line of regression calculated for all small laboratory animals (Fig. 1).

Within the genus of hamster, four species were available. The advantage of choosing four genetically different species was the inherent large weight range covered by these species. Disadvantageous was the non-simultaneous maturity of the various species. Unlike the three other hamster species, *Cricetus cricetus,* was according to its growing curve not considered adult at 100 days of age. As a result, kidney and body mass of this species were determined when males and females had reached adulthood at 204 days. Whether this peculiarity of *Cricetus cricetus* is responsible for mean values far below the overall regression line remains unclear (Fig. 1). The values of the three hamster species reaching adulthood at 100 days plot well along the general regression for all species investigated. No significant difference is apparent between the allometric function of males and females. Variation among females was, however, larger. This resulted in larger standard deviations of the mass coefficient and exponent and in a reduced correlation coefficient "r" (Table 2). The mass exponents are lower than those found in the interspecific relationship. This difference in slope remains insignificant due to the small number of hamster species investigated. It should be noted, however, that additional species of larger laboratory hamsters are not available.

Within the different strains of rats, genetic as well as ontogenetic allometry was determined. Although genetic variation in body mass between strains was large, highly significant correlations were found. Within females as well as males, the mass coefficient and the mass exponent did not differ significantly from those found in the interspecific relationship (Prothero 1984). Furthermore, no significant sex difference exists between the allometric functions computed for males and females.

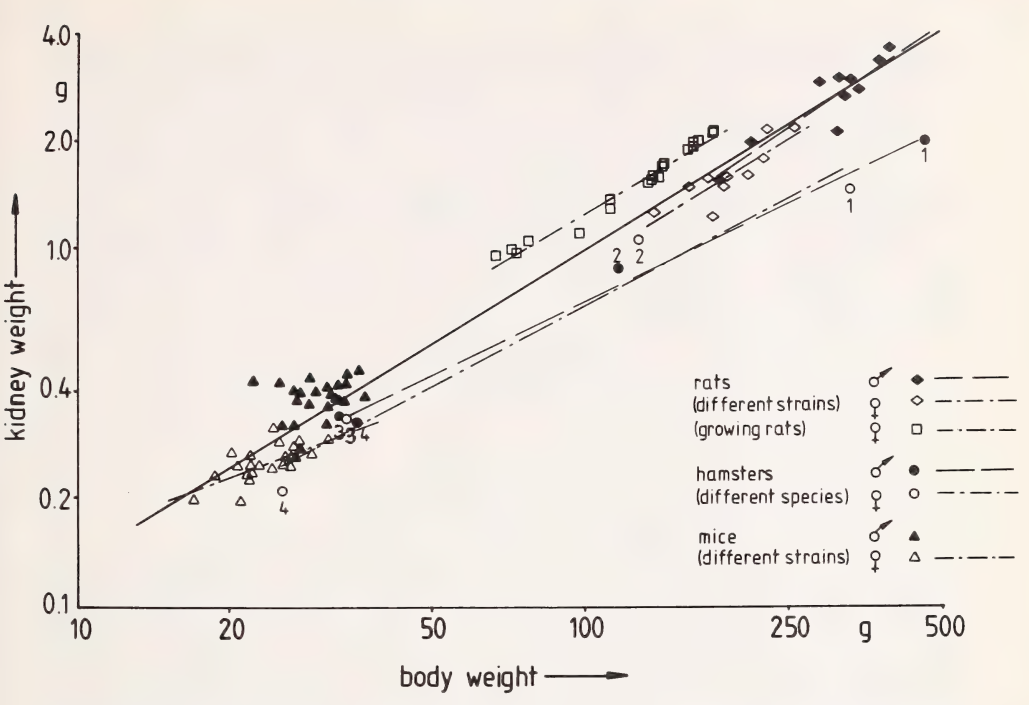


Fig. 1. Intra- and interspecific allometry of kidney mass to body mass. Intraspecific (rats and mice): open triangles = female mice; solid triangles = male mice; open diamonds = female rats; solid diamonds = male rats. – Ontogenetic (rats): open squares = growing female rats. – Interspecific (hamster): open circles = female hamster; solid circle = male hamster. 1: *Cricetus cricetus;* 2: *Mesocricetus auratus;* 3: *Phodopus sungorus;* 4: *Cricetulus griseus.* Dashed lines = males

Growing rats of the inbred strain investigated cover a wide range of body weight (67–180 g). Within this inbred strain less variation is apparent when growing individuals were compared as between different strains. This small variance across the ontogenetic function is evident in the small standard deviation of the mass coefficient and exponent. The mass exponent is equivalent to that of the interspecific comparison. The line of the regression, however, appears shifted, even though there is no statistical difference between the mass coefficient of the ontogenetic and the intra- and interspecific allometries.

Consideration of all measured data (95 individual values taken from both sexes of six different species) in the "interspecific" (mouse-rat-hamster) allometric analysis, without selection or exclusion of data, results in an allometric function (Table 2) that is surprisingly close to the regression previously found by comparing 1105 animals from 63 species (Prothero 1984). This indicates that animals lying in the relativ narrow weight range from 20 to 500 g follow the same allometric function as described for much larger species. It does not, however, coincide with published data concerning oxygen consumption, whereby animals less than 260 grams follow a different regression than those greater than 260 grams (Bartels 1982).

Moreover, the present analysis is an example of the caution needed in interpretation of intraspecific allometries. Even though intraspecific variance can be statistically reduced to genetic or ontogenetic variation through exclusion of environmental influences, resulting allometries in these smaller species are often unreliable.

Nevertheless, the Figure 1 indicates a clear similarity between the intraspecific regression of laboratory species investigated and the common interspecific regression. Intra-

specific deviations from the general allometric function appear to be more a function of excessive variation than a systematic trend inherent in intraspecific allometry. The mass coefficients of the different species are not significantly different from those in the interspecific allometric function. Thus, no obivous generalized discrepancy is apparent between intraspecific and interspecific kidney to body mass allometry. In contrast to kidney mass, energy metabolism (HEUSNER 1982) and brain mass (RÖHRS 1961) follow different slopes of regression in intra- and interspecific allometries.

In conclusion, the allometric relationship of kidney mass to body mass seems genetically determined as a quantitative, multivariate trait. This genetic trait is responsible for genetic variation within a single species, during the period of growth, as well as for the differentiation between species.

Acknowledgement

This study was supported by Deutsche Forschungsgemeinschaft HA 1146/2-1.

Zusammenfassung

Intraspezifische Allometrie: Die Niere

Inter- und intraspezifische Allometrien von Nieren- zu Körpergewicht wurden an Hand von 4 Hamsterspezies, 10 Ratteninzuchtstämmen und 24 Mäuseinzuchtstämmen bestimmt. Die Bestimmung genetischer Allometrien war möglich durch eine Reduktion auf ausschließlich genetische Varianz durch die Verwendung von Merkmalsmittelwerten der einzelnen Spezies bzw. Inzuchtstämme an Stelle der Einzelwerte. Ontogenetische Allometrie wurde ermittelt an Hand von wachsenden weiblichen Individuen eines einzelnen Inzuchtstammes.

Sämtliche Inter- und Intra-Spezies-Allometrien von Nieren- zu Körpergewicht sind signifikant mit der einen Ausnahme der Intra-Spezies-Allometrie der männlichen Mäuse. Diese Ausnahme kann durch eine extreme genetische Variation zwischen den Mäuseinzuchtstämmen in Verbindung mit dem nur schmalen Körpergewichtsbereich erklärt werden.

Innerhalb der Spezies Ratte ergeben sich statistisch signifikante Allometrien. Die genetischen Allometriefunktionen (Allometrieexponent bei den Männchen 0,96, bei den Weibchen 0,98) sind equivalent der Inter-Spezies-Allometrie (PROTHERO 1984). Ähnlich vergleichbar ist auch die ontogenetische Allometrie (Allometrieexponent 0,82), so daß die Intra-Spezies-Werte für Allometrieexponenten und -koeffizienten sich nicht von denen der Intra- und Inter-Spezies-Allometrien unterscheiden.

Weiterhin zeigen die vorliegenden Untersuchungen, daß die erstellte Maus-Hamster-Ratte-Allometrie mit einem Allometrieexponenten von 0,86 der an Hand von 63 verschiedenen Spezies von Landsäugetieren (Allometrieexponent 0,85, PROTHERO 1984) gleicht. Daraus folgt, daß die allgemeine Intra-Spezies-Allometrie von Nieren- zu Körpergewicht für Säugetierspezies verläßlich und auch für den Inter- und Intra-Spezies-Vergleich kleiner Versuchstiernager tauglich ist.

Literature

BARTELS, H. (1982): Metabolic rates of mammals equals the 0.75 power of their body weight? Experim. Biol. and Medicine **7**, 1–11.

BRODY, F. (1945): Bioenergetics and Growth. New York: Reinhold Publ. Corp.

CALDER, W. A. III.; BRAUN, E. J. (1983): Scaling of osmotic regulation in mammals and birds. Am. J. Physiol. **244**, R 601–R 606.

CLOSKEY, G. M.; JERMANOWICH, N. B. (1985): Correspondence to the editor. Lab. Anim. Sci. **35**, 363.

CRABTREE, C. (1941): The structure of Bowman's capsule in castrate and testosterone treated male mice as index of hormonal effects on renal cortex. Endocrinology **29**, 197–203.

HACKBARTH, H.; HACKBARTH, D. (1981): Genetic analysis of renal function in mice: 1. Glomerular filtration rate and its correlation with body and kidney weight. Lab. Animals **15**, 267–272.

— (1982): Genetic analysis of renal function in mice: 2. Strain differences of sodium, potassium, osmolar and free water clearances and their correlation with body and kidney weight. Lab. Animals **16**, 27–32.

HACKBARTH, H.; BAUNACK, E.; WINN, M. (1981): Strain differences in kidney function of inbred rats: 1. Glomerular filtration rate and renal plasma flow. Lab. Animals **15**, 125–128.

Hackbarth, H.; Büttner, D.; Gärtner, K. (1982): Intraspecies allometry: correlation between kidney weight and glomerular filtration rate vs. body weight. Am. J. Physiol. **242,** R 303–R 305.

Heusner, A. A. (1982): Energy metabolism and body size. I. Is the 0.75 mass exponent of Kleiber's equation a statistical artifact? Resp. Physiol. **48,** 1–12.

Hutson, J. M.; Holt, A. B.; Egami, K.; Niall, M.; Fowler, R.; Check, D. B. (1981): Compensatory renal growth in the mouse. I. Allometric approach to the effect of age. Ped. Res. **15,** 1370–1374.

Huxley, J. (1932): Problems of relative growth. London: Methuen.

Kittelson, J. A. (1917): The postnatal growth of the kidney of albino rats with observation on an adult human kidney. Anat. Rec. **13,** 385–408.

Prothero, J. (1984): Organ scaling in mammals: the kidneys. Comp. Biochem. Physiol. **77 A,** 133–138.

Röhrs, M. (1959): Neue Ergebnisse und Probleme der Allometrieforschung. Z. wiss. Zool. **162,** 1–95.

Röhrs, M. (1961): Allometrie und Systematik. Z. Säugetierkunde **26,** 130–137.

Rytand, D. A. (1938): The number and size of mammalian glomeruli as related to kidney and body weight, with methods for their enumeration and measurement. Am. J. Anat. **62,** 502–520.

Sachs, L. (1984): Applied Statistics. A Handbook of techniques. New York, Heidelberg, Berlin: Springer.

Stahl, W. R. (1965): Organ weights in primates and other mammals. Science **150,** 1039–1042.

Authors' address: PD Dr. H. Hackbarth and Prof. Dr. K. Gärtner, Zentrales Tierlaboratorium und Institut für Versuchstierkunde, Medizinische Hochschule Hannover, Konstanty-Gutschow-Str. 9, D-3000 Hannover 61, FRG

Protokoll über die Mitgliederversammlung der Deutschen Gesellschaft für Säugetierkunde e. V. am 11. September 1989 im Vortragssaal des „Collège Propédeutique“ der Universität Lausanne

Der 1. Vorsitzende, Herr KULZER, eröffnet die Versammlung um 16.20 Uhr.

1. Die Tagesordnung wird angenommen.
2. Herr KULZER gibt bekannt, daß die Verlagsbuchhandlung Paul Parey drei Buchprämien für die besten Poster ausgesetzt hat und dankt ihr für dieses Entgegenkommen.
3. Herr SCHMIDT verliest den Bericht über das abgelaufene Geschäftsjahr 1988. Im Berichtsjahr erschien der 53. Band der „Zeitschrift für Säugetierkunde“ in sechs Heften mit 384 Seiten. Zusätzlich wurde allen Mitgliedern das Sonderheft mit den Kurzfassungen der Vorträge und Posterbeiträge der Tagung in Münster zugesandt. Dankenswerterweise hat sich die Verlagsbuchhandlung Paul Parey bereit erklärt, die Zeitschrift – ohne Mehrkosten – ab Heft 4/1989 um jeweils acht Druckseiten pro Heft zu erweitern. Obgleich damit ein schnelleres Erscheinen der eingereichten Arbeiten ermöglicht wird, werden die Autoren dringend gebeten, sich künftig verstärkt der „Wissenschaftlichen Kurzmitteilungen“ zu bedienen.
   Auf Einladung von Herrn BERGER, Westfälisches Museum für Naturkunde, fand die 62. Hauptversammlung der Gesellschaft vom 2. bis 6. Oktober 1988 in Münster statt. Aus diesem Anlaß wurde der Förderpreis an Herrn Dr. VOLKER SOMMER verliehen. Die Mitglieder werden gebeten, dem Geschäftsführer möglichst bald geeignete Preisträger zu nennen, damit der „Fritz-Frank-Preis“ 1990 wieder vergeben werden kann. 1989 wurde keine Arbeit den strengen Anforderungen des Stifters gerecht, die Preisverleihung mußte daher entfallen.
   Durch den Tod verlor die Gesellschaft folgende Mitglieder:
   Prof. Dr. FRANZ PETER MÖHRES, Tübingen,
   Dr. OTTO SCHULZ-KAMPFHENKEL, Hamburg,
   Im Jahre 1988 hatte die Gesellschaft 613 Mitglieder.
4. Da Frau KÜHNRICH an der Teilnahme verhindert ist, erläutert Herr SCHMIDT den von ihr vorgelegten ausführlichen Jahresabschluß und dankt ihr und der Verlagsbuchhandlung Paul Parey für den fortwährenden Einsatz zum Wohle der Gesellschaft. Der Vorschlag des Vorstandes, die Zeitschrift für Säugetierkunde künftig nur noch für ein Jahr bereitzuhalten, um auf diese Weise die Zahlungsmoral der Mitglieder zu verbessern, wird einstimmig angenommen.
5. Die Kassenprüfer Herr BOHLKEN und Herr SCHLIEMANN haben keinen Anlaß zu Beanstandungen gefunden.
6. Die Anträge zur Entlastung des Schatzmeisters und des Vorstandes werden einstimmig angenommen.
7. Als Kassenprüfer für das Geschäftsjahr 1989 werden die Herren BOHLKEN und SCHLIEMANN wiedergewählt.
8. Der Vorstand sieht keine Veranlassung zur Veränderung der Mitgliedsbeiträge. Sie betragen DM 95,– für Vollmitglieder, DM 60,– für Studenten und DM 10,– für Ehepartner. Die Versammlung schließt sich dieser Auffassung einstimmig an.
9. Die Mitglieder nehmen die Einladung der Herren SCHROEPFER und EVERTS an, die 64. Hauptversammlung vom 23. bis 27. September 1990 in Osnabrück abzuhalten. Als Schwerpunktthemen werden „Ontogenie“, „Ernährung und Verdauung“ und „Ökologie der Mammalia“ gewählt. Die Einladung von Herrn SCHLIEMANN, 1991 in Hamburg zu tagen, wird durch Akklamation angenommen.

10. Der Versammlung wird bekanntgegeben, daß die Herren HERRE und STARCK mit Wirkung vom 31. 12. 1989 als Herausgeber der „Zeitschrift für Säugetierkunde“ auf ihren eigenen Wunsch entpflichtet werden. Unter dem Beifall der Versammlung spricht ihnen der Vorstand den Dank für die langjährige und wertvolle Mitarbeit aus. Herr LANGER tritt ab 1. 1. 1990 in die Schriftleitung der Zeitschrift ein.
11. Die Mitglieder werden gebeten, dem Vorstand Autoren zu nennen, die für KEVIN STERLINGS „International History of Mammalogy“ einen Beitrag zur Geschichte der Säugetierkunde in Deutschland liefern können.
12. Die Sitzung endet um 18.20 Uhr.

Prof. Dr. E. KULZER, 1. Vorsitzender — Prof. Dr. U. SCHMIDT, Geschäftsführer — Dr. H. FRÄDRICH, Schriftführer

Ausschreibung des FRITZ-FRANK-Preises
Förderpreis der Deutschen Gesellschaft für Säugetierkunde

Die Deutsche Gesellschaft für Säugetierkunde schreibt den Förderpreis in Höhe von 3000,– DM als Anerkennung für hervorragende wissenschaftliche Leistungen junger Forscher aus.

Voraussetzung ist eine im Druck vorliegende Arbeit aus den Gebieten **Phylogenie** und **Systematik, Verbreitung, Ethologie, Ökologie** oder **Populationsbiologie** der Säugetiere. Die Arbeit muß in den 3 vorausgehenden Kalenderjahren erschienen sein. Die Autoren dürfen beim Erscheinen der Arbeit nicht älter als 33 Jahre sein.

Bewerbungen oder Vorschläge erbitten wir an die Geschäftsstelle der Gesellschaft: Prof. Dr. U. SCHMIDT, Zoologisches Institut, Poppelsdorfer Schloß, D-5300 Bonn 1, unter Beifügung von 5 Sonderdrucken.

Der Jury gehören Wissenschaftler verschiedener Universitäten und Mitglieder der Gesellschaft an.

Der Preis wird bei der Eröffnung der Jahresversammlung der Gesellschaft in Osnabrück (23.–27. 9. 1990) überreicht.

Internationale Kommission für Zoologische Nomenklatur

The following opinion has been published by the International Commission on Zoological Nomenclature in the Bulletin of Zoological Nomenclature:

Vol. 46, part 3, 29 March 1989

1535 *Halianassa studeri* von Meyer, 1838 (Mammalia, Sirenia): neotype designated; and *Halitherium* Kaup, 1838 (Mammalia, Sirenia): *Pugmeodon schinzii* Kaup, 1838 designated as the type species

TURNER, D.; BATESON, P. (Hrsg.): **Die domestizierte Katze.** Eine wissenschaftliche Betrachtung ihres Verhaltens. Rüschlikon-Zürich, Stuttgart, Wien: Albert Müller Verlag. 259 S., zahlreiche Abbildungen, Zeichnungen und Tabellen. Leinen, DM 79,–. ISBN 3-275-00431-1

Dieses Buch ist das Ergebnis eines Symposiums über das Verhalten der Katze. Die Herausgeber haben sich zum Ziel gesetzt, damit nicht nur den Wissenschaftler, sondern auch den interessierten Laien anzusprechen. Das hat sich m. E. in mancher Hinsicht als problematisch erwiesen, denn während bei drei der vier verschiedenen Themenbereiche, denen die einzelnen wohl aufeinander abgestimmten Beiträge zugeordnet sind, die Katze eindeutig im Mittelpunkt steht – sie betreffen die Jugendentwicklung, das Sozialleben und das Beutefangverhalten –, behandelt der vierte Abschnitt vor allem die Beziehungen zwischen Katze und Mensch. So gibt das von C. MERTENS und R. SCHÄR verfaßte und hier eingeordnete Kapitel „Praktische Aspekte der Forschung an Katzen" wertvolle Hinweise und Hilfen für eine artgerechte Haltung dieser Tiere, aber es ist zu fragen, ob es auch Bestandteil einer wissenschaftlichen Betrachtung sein sollte. Damit ist ein Einwand vorgebracht, der verschiedentlich auch an anderer Stelle gilt: So mag es ein Zugeständnis an ein breites Publikum sein, wenn z. B. von „wildlebenden, also nicht an ein Heim gebundenen Katern" und „domestizierten Weibchen" die Rede ist (S. 141), aber auf diese Weise geraten klar definierte Begriffe durcheinander.

Das Kapitel „Domestikation und Entwicklungsgeschichte der Katze" von A. SERPELL gibt in weiten Bereichen die Einstellung des Menschen zur Katze im Laufe der Geschichte wieder, behandelt also mehr diese Entwicklung im menschlichen Verhalten gegenüber der Katze als deren Entwicklungsgeschichte selbst. An anderer Stelle behauptet SERPELL, daß die Katze einigermaßen resistent gegenüber Extremzüchtungen sei, doch weist er selbst darauf hin, daß die Katze verglichen mit dem Hund noch nicht lange auf spezifische Eigenschaften hin gezüchtet wird (S. 183).

Trotz dieser Anmerkungen ist insgesamt herauszustellen, daß die einzelnen Bearbeiter in ihren Beiträgen neben der Darstellung eigener Ergebnisse eine breite Übersicht mit einer Fülle von Literaturzitaten über das jeweilige Arbeitsgebiet geben. Die klare Gliederung der Kapitel sowie ein Stichwortregister erleichtern die Benutzung des Buches.

D. HEINRICH, Kiel

CZERNAY, S.: **Spießhirsche und Pudus.** Die Gattungen *Mazama* und *Pudu*. Die Neue Brehm-Bücherei 581. Wittenberg-Lutherstadt A. Ziemsen Verlag 1987. 84 S., 44 Abb., 6 Tab. DM 13,20. ISBN 3-7403-0046-9

Der Autor, der sich mit *Pudu pudu* im Zoopark Erfurt beschäftigt hat, schildert im vorliegenden Bändchen die südamerikanischen Zwerghirsche vor allem aufgrund der spärlichen Literatur seit der Entdeckungsgeschichte. Nach einer kurzen allgemeinen Charakteristik behandelt er die acht Arten jeweils in der Folge: Nomenklatur und Trivialnamen, Merkmale, Verbreitung und Habitat, Lebensweise, Parasiten und Bejagung. Das Buch schließt mit Angaben über die Bedeutung für den Menschen, die Haltung und den gesetzlichen Schutz. Die Abbildungen sind ganz überwiegend Schwarzweißfotos von Habitus, Schädeln und Lebensraum. Außerdem findet man grobe Verbreitungskarten, in die auch die Unterarten eingetragen sind.

Wenn noch kein sehr geschlossenes Bild entsteht, beruht das auf dem eher mageren Wissenstand. Die vorhandene Literatur ist im wesentlichen verarbeitet. So findet man einige Angaben zum Geweihzyklus, der oft nicht mit der Jahresperiodik übereinstimmt und auch von der Fortpflanzung ziemlich unabhängig zu sein scheint. Die Beschreibung des NF-Wertes als „Anzahl der großen Chromosomenenden" ist verwirrend. Im allgemeinen ist der Text aber verständlich und ermöglicht eine rasche Orientierung.

J. NIETHAMMER, Bonn

Deutsche Gesellschaft für Säugetierkunde: Referate, Vorträge und Posterdemonstrationen der 63. Hauptversammlung 1989

Ein Hauptziel der Deutschen Gesellschaft für Säugetierkunde ist, auf ihren Jahrestagungen über Säugetiere arbeitende Wissenschaftler verschiedenster Fachrichtungen zusammenzuführen, den Gedanken- und Erfahrungsaustausch anzuregen, um so Erkenntnisse aus den einzelnen Forschungsgebieten zu integrieren. Die Referate und Posterdemonstrationen auf der 63. Hauptversammlung geben das Spektrum der Fachrichtungen innerhalb der Säugetierkunde wieder und zeigen Beziehungen zu anderen Disziplinen auf. Die Hauptversammlung 1989 wurde gemeinsam mit der Schweizerischen Gesellschaft für Wildforschung in Lausanne durchgeführt. Traditionsgemäß wurden drei Themenschwerpunkte festgelegt. Schwerpunkt »Endokrinologie und Neurohormone der Säugetiere« ist im physiologischen Bereich angesiedelt. Der Schwerpunkt »Einsatz der telemetrischen Methoden in der Säugetierforschung« betrifft Techniken im Bereich der Neurologie (z. B. Elektroencephalogramme), Physiologie (Thermoregulation) und Ökologie (Ortung von Tieren im Raum). Mit dem Schwerpunkt »Wildlife-Management und Ökologie der Säugetierkunde« soll ein Problem zur Sprache kommen, das Säugetierkundler wie Wildbiologen betrifft. Kurzfassungen der Vorträge und Posterdemonstrationen der Deutschen Gesellschaft für Säugetierkunde sind ab der 58. Hauptversammlung 1984 in Göttingen noch lieferbar. Zu beziehen durch jede Buchhandlung.

★ **Deutsche Gesellschaft für Säugetierkunde, 63. Hauptversammlung in Lausanne, 10. bis 14. September 1989.** Kurzfassungen der Vorträge und Posterdemonstrationen. Herausgegeben von Dr. Christel Schmidt, Bonn, und Prof. Dr. Peter Vogel, Lausanne. 1989. 50 Seiten. Kartoniert 24,– DM

Verlag Paul Parey · Spitalerstraße 12 · 2000 Hamburg 1

PAUL PAREY

Subscription information for USA, Canada and Mexiko obtainable from Paul Parey Scientific Publishers/IR Unltd., 35 West 38th Street, Suite 3 W, New York, NY 10018, USA.

Erscheinungsweise und Bezugspreis 1989: 6 Hefte bilden einen Band. Jahresabonnement Inland: 318,– DM zuzüglich 13,80 DM Versandkosten, Gesamtpreis 331,80 DM einschließlich 7 % Mehrwertsteuer. Jahresabonnement Ausland: 318,– DM zuzüglich 18,– DM Versandkosten. Das Abonnement wird zum Jahresanfang berechnet und zur Zahlung fällig. Es verlängert sich stillschweigend, wenn nicht spätestens am 15. November eine Abbestellung im Verlag vorliegt. Die Zeitschrift kann bei jeder Buchhandlung oder bei der Verlagsbuchhandlung Paul Parey, Spitalerstraße 12, D-2000 Hamburg 1, bestellt werden. Die Mitglieder der „Deutschen Gesellschaft für Säugetierkunde" erhalten die Zeitschrift unberechnet im Rahmen des Mitgliedsbeitrages.

Z. Säugetierkunde 54 (1989) 6, 337–408







